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**W. G. FARLOW**







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ASSISTANT PROFESSOR OF BOTANY IN UNIVERSITY COLLEGE, LONDON.

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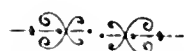
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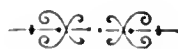








Fig. 1.



Fig. 2.

Fig. 1.—The Wonderboom (*Ficus cordata*) at the foot of the Magaliesberg, near Pretoria. From a photograph by Professor R. H. YAPP.

Fig. 2.—View of the interior of the Wonderboom, showing one of the now decumbent branches which has become rooted and has given rise to a new stem.



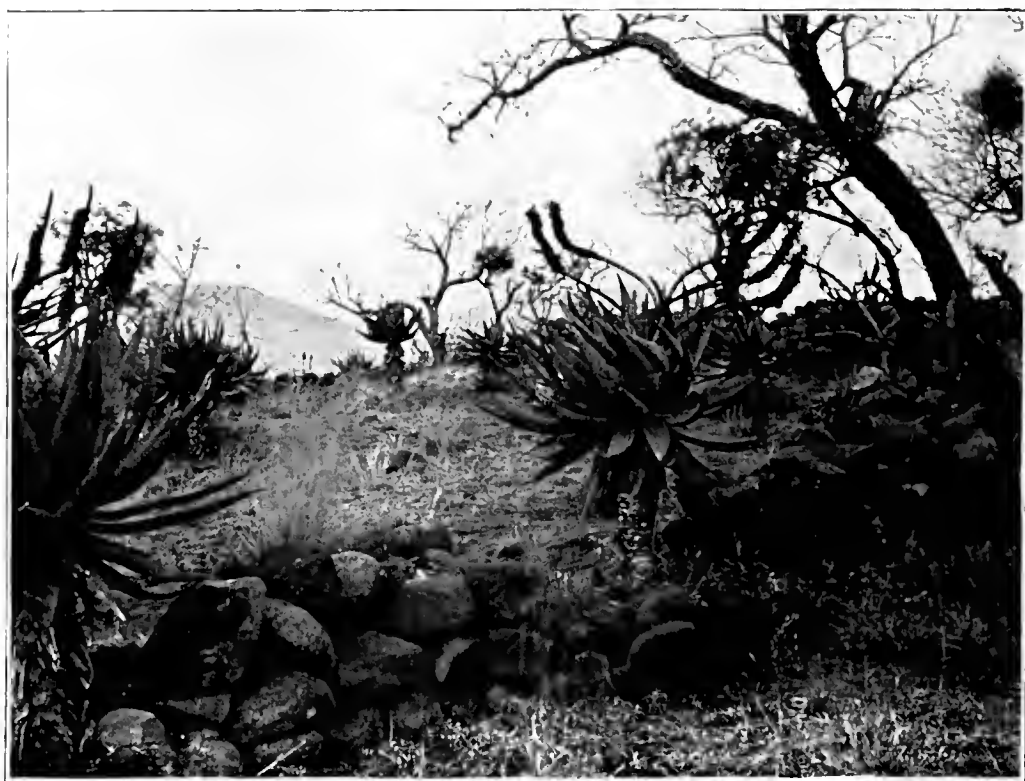


Fig. 3.



Fig. 4.



Fig. 5.

Fig. 3. Group of Aloes from Hlangwane Hill, near Colenso. (From a photograph by Prof. R. H. Yapp.)

Fig. 4. *Vellozia* sp., common on the High Veld of the Transvaal, with hard brown stem and drought-resisting leaves.

Fig. 5. *Myrothamnus flabellifolia*, with leaves (a) expanded (b) closed.

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SKETCHES OF VEGETATION AT HOME  
AND ABROAD.

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II.—SOME ASPECTS OF THE VEGETATION OF SOUTH AFRICA.

BY F. E. WEISS, D.Sc.

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PART II.—NATAL AND THE TRANSVAAL.

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[PLATES I. AND II. AND TEXT-FIGS. 1—3.]

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WHILE the Cape Peninsula has a very marked winter rainfall, we find as we pass eastward along the south coast of Africa, a gradual equalisation of summer and winter rainfalls. This more evenly distributed precipitation, amounting often to nearly thirty inches, has favoured a tree-like vegetation in many districts, and one of these forests covering a large area in the Knysna district yields a considerable amount of timber, largely the so-called yellow wood (*Podocarpus*), the stinkwood (*Ocotea*) and the black ironwood (*Olea laurifolia*).

Eastward of Port Elizabeth we come upon the region of predominating summer rains, and the flora here has a much more luxuriant aspect than in the South Western region, it is in fact merely an outlier of that of Tropical Africa. This East coast region including all the lower lying portions of Natal and the Eastern portion of Cape Colony, though very distinct from the South-Western coast region, goes over very gradually into the latter. It is characterised by the deficiency or absence of Proteaceae and Ericaceae so typical of the Cape Peninsula, while certain families characteristic of the tropics of Africa and India, such as the Myrtaceae, Rubiaceae and Asclepiadaceae begin to assume considerable proportions in the vegetation. On the other hand, some remnants

of a very ancient flora are preserved in this region in the Cycads *Encephalartos* and *Stangeria*. The former, called "Kaffir Bread," is found in the Eastern parts of Cape Colony, while the latter is confined to Natal. There is no doubt that these forms represent the remainder of a very ancient group of plants, with a world-wide distribution in Mesozoic times.

As regards the general aspect of the vegetation close along the coast of this South Eastern region we find an area of forest land established under conditions of adequate supply of summer rains and a higher temperature due to the warm Mozambique current which flows along the East Coast. This more tropical climate has enabled palms such as *Phoenix reclinata* and *Hyphaene coriacea* to establish themselves in this littoral zone as far South and East as Port Elizabeth. The forest-areas contain also tree-ferns (*Hemitelia*) and aerial orchids in districts where the rainfall is sufficiently abundant, as it is in the more Northern portion of this region. Another characteristic plant is the tall *Strelitzia augusta*, the pale flowers of which are pollinated by birds of the Cynnaris group, which alight on the arrow-shaped organ projecting from the flower. A further tropical aspect is given to the Natal Coast by the occurrence of a Mangrove vegetation such as the members of the British Association were privileged to visit near Durban.

Inland from the littoral forest-belt, formerly no doubt much more extensive, on the rising lands there was formerly a thorn bush which like the forest land has had to give way to the successful agricultural development of Natal.

Around Durban one sees large plantations of Pineapples, while both the Mangoes, Bananas and Pawpaws yield abundant crops. 4,000 acres are under cultivation for tea and yield about two million pounds per annum. The tea industry dates back to 1850, when the first plants, probably of China tea, were introduced from Kew. Since then a considerable number of Indian varieties have been grown.

The sugar cane on the other hand seems to have been a native of Natal and to have been grown in small quantities about the kraals of the Zulus. Now sugar planting has become the most important industry of Natal and produces £600,000 of sugar. But while these crops flourish in the littoral belt, where the rainfall is abundant [it is  $42\frac{1}{2}$  inches (1,000 mm.) at Durban], as we proceed upwards towards the central plateau these crops can no longer be raised. We pass from a belt of land in which temperature and

rainfall make forest land possible to grass land such as is met with on the hills and on the upland round Petermaritzburg. Trees here are confined to the valleys and river-banks, while on the exposed uplands the grassland is only here and there dominated by succulent tree-aloes such as those seen around the back of Fort Wylie near Colenso, and on Waggon Hill near Ladysmith (see Pl. 2, fig. 3). Other Monocotyledons found in the grass veld possess underground bulbs or corms and lose their vegetative organs during the adverse winter season. Of these plants, which detract somewhat from the feeding value of the pasturage when very abundant, various forms of brightly coloured *Ixia* seemed to be the most common during our visit to the higher portions of Natal.

As stated before, in these uplands trees are mainly restricted to the water courses and consist for the most part of various species of *Acacia*. Some Australian trees however have been introduced, partly as shade trees and partly on account of their timber. They are drought resisting trees such as various forms of *Eucalyptus*, the Australian Silk-Oak (*Grevillea robusta*) and the graceful She-Oak (*Casuarina*), the latter having at a distance the appearance of a delicate leaved pine with pendant branches. But the most useful of all the introduced trees is undoubtedly the Black Wattle (*Acacia decurrens*). It is calculated that the plantations of the tree embrace about 25,000 acres and yield a yearly return of £100,000, for besides a large export of the bark for tanning purposes, nearly 20,000 tons of mining props are exported for use in the Transvaal Mines.

Those parts of Natal on the East slopes of the Drakensberg range, which lie at an altitude of 4,000 ft. and upwards, are included by Dr. Bolus in the Kalahari Region, of which they form the Eastern portion, while the Western portion includes the whole of the Orange River Colony, the Transvaal and Bechuana Land. This Western portion represents a wide inland basin 3,000-ft. to 6,000-ft. above the sea level, and drained mainly by the Orange River and its tributaries, while the narrow Eastern portion has shorter and more rapidly running rivers which empty themselves into the Indian Ocean.

The rainfall in this region, mainly due to Summer rains, varies very considerably, decreasing greatly as we pass westward from the High Drakensberg range, until we get ultimately into the Western Kalahari desert where the rainfall is less than 5 inches per annum. The vegetation is therefore naturally very varied. In the ravines to the East of the Drakensberg mountains are forests, while the "High Veld" to the West is a grass steppe. The climate of this

region is, owing to its altitude, fairly rigorous, with sharp frosts at night during the winter months, and always a considerable difference between the day and night temperatures. The absence of trees, and even of shrubs except in the moister and warmer shallow valleys, gives a very monotonous appearance to the landscape, especially at the end of the dry season when most of the bulbous and tuberous plants have died down. Here and there a few low growing composites, including several *Helichrysa*, are to be seen in flower, and in some places a handsome *Lobostemon*, nearly two feet in height, with large inflorescences of pale bell-shaped flowers. One of the most striking plants of this grass veld was a species of *Vellozia* (Pl. 2, fig. 4) with a short brown stem often charred by grass-fires. The unbranched stem, about eighteen inches in height, and nearly two inches in diameter, is densely covered with the dead leaf-bases, which render the plant very drought-resisting, and even protected against fire. Near the top it bears a tuft of greyish-green leaves of very tough and resistant nature. In the dry season the leaves are folded sharply along the mid-rib so as to be V-shaped in transverse section, and both the upper and lower surfaces are deeply grooved, the stomata opening into these depressions. It does not seem to possess any definite motor-cells which cause an unfolding of the leaf; but when placed in water its tissues swell, owing no doubt to the mucilaginous sap which many of its cells contain. As the Summer rains had not commenced in the Transvaal these *Vellozias* were not generally in flower, and only on one stump did we find the purple flowers of this curious Monocotyledon.

The monotony of the grass-veld was also broken by the nests of White-ants (*Termites*) dotted about over the plain, their earth-built mounds, two or three feet in height, being often opened out by the Cape Ant-Eater, or Aard-vark, a large animal of nocturnal habits which feeds on the ants in the termitaria. Occasionally we saw growing from the top of a ruined or forsaken nest a tuft of *Agaries*, due no doubt to the exuberant growth of the fungus which many of the termites cultivate for food, as do the leaf-cutting ants of the tropics. This curious habit of the white ants was first suggested by Smeathman<sup>1</sup> in 1781, and has recently been confirmed by Haviland<sup>2</sup> for several species of South African termites.

Such is the character of the High Veld or Grass Veld stretching from the foot of the Drakensberg Range to Johannesburg. Passing

<sup>1</sup> Smeathman. Phil. Trans., Vol. LXXI., 1781.

<sup>2</sup> Haviland, G. D. Observations on Termites, Journ. Linn. Soc., Vol. XXVI., 1898.



to Pretoria we come not only to a lower altitude, but also into the drainage area of the Limpopo, and beyond the Magaliesberg Range we enter the Low-veld or "Bush veld" which stretches Northward and Westward. This is practically a savannah, *i.e.* a grass-covered country with scattered trees and often of park-like aspect. Where sufficiently watered or irrigated it is capable of yielding an abundant harvest of maize, tobacco, oranges, lemons, and even bananas.

Just outside Pretoria, on the Magaliesberg, to which Mr. Burt-Davy had been good enough to arrange an excursion, we had an opportunity of seeing some of the Transvaal tree vegetation, including the Kaffirboom (*Erythrina caffra*), its leafless branches terminated by magnificent bunches of scarlet flowers which are pollinated by birds. The long papilionaceous flowers are directed stiffly back from the ends of the twig, like points of an arrowhead, and the bird, alighting on the branch somewhat below the flower, thrusts its beak between the brilliant petals, which are nearly two inches in length. In addition the Northern slope of the Magaliesberg Range was clad with numerous trees, including several species of *Combretum* with large winged fruits, and Dombeyas with clusters of white flowers.

But the tree of greatest interest to botanists, as well as other visitors, was the "Wonderboom" at the foot of the hill, a specimen of *Ficus cordata*, forming a dense and dark green grove in great contrast to the leafless trees on the slopes (Pl. I, fig. 1). The original tree has in part died away, but not before its large branches had fallen over and become rooted fifteen or more feet from the parent stem, producing a number of new trees around the centre (Pl. I, fig. 2). And the trees of this second ring have produced yet a third and more numerous series in a similar way on the outside, so that the original tree is now replaced by a grove of vegetative descendants, which from the outside appear as a single wide-spreading tree.

Many of the smaller plants found on this memorable excursion were of great interest to us, such as the unisexual and dioecious Labiate *Moschosma*, a rubber vine *Landolphia capensis*, and numerous hard leaved Aloes which, with the little *Selaginella rupestris*, covered the drier rock faces. But the most remarkable of all these xerophytic plants was the shrubby *Myrothamnus flabellifolia*, a plant largely distributed over the mountains in Central Africa, where it ascends to a great height and is often the last shrub, often creeping like *Salix repens*. As we saw it in the dry

season its leaves were closely folded like small fans and curved up over the growing points (Pl. 2, fig. 5b), while the branches even bent upwards so that the main shoots had almost the appearance of birch rods. The surface of the leaves is strongly pigmented with anthocyanin, which is no doubt useful to the plant as a protection against excessive insolation during the period of drought. After the first rains, the leaves open out fresh and green (fig. 5a), and the appearance of the shrub undergoes a remarkable change. Even branches which have been gathered four months ago revive in what seems a miraculous manner when placed in water for a day or two, and appear quite fresh and living. As in the *Vellozia* mentioned above, there seem to be no special groups of motor cells to effect the opening of these fan-shaped leaves as there are in the xerophytic grasses of moorlands and sand hills, but the leaf as a whole becomes turgid and swells up, thereby becoming partially flattened. As a protection for the axillary buds the leaf bases of the opposite leaves are fused into a sheath which persists even after the leaf-blades have fallen away. This plant is also characterised by the possession of numerous oil glands in its epidermis, which may possibly be of service in lessening the evaporation, as has been suggested for some Labiatae possessing similar glands.

A six days trek across the Transvaal from Pretoria to Mafeking through the Rustenburg and Marico districts gave us an opportunity of becoming acquainted with some portions of the Bushveld which have great agricultural possibilities as soon as extensive irrigation works supply the necessary water, and a projected light railway renders the Johannesburg market accessible to the farmers. At present except for small irrigated portions the district is mainly given over to cattle farming, and unfortunately Horse Sickness and the East Coast Tick Fever have of late years proved very disastrous to the live stock.

Extensive grass fires, too, started in parts to destroy the cattle ticks which are the carriers of disease, have caused some destruction to the trees, and, if persisted in, are likely to decrease considerably not only the number of trees, but, by doing so, also the water storing capacity of the country. In addition to the trees we had seen on the slopes of the Magaliesburg, and which we found again in the bushveld, we noticed numerous sugar-bushes (*Proteas*) in some parts, and even more frequently the Proteaceous tree *Faurea saligna* with willow-like foliage (see fig. 1). This handsome tree with its pendant evergreen leaves was not infrequently infested by a *Loranthus*

with long tubular and purple flowers no doubt adapted, like other South African species of this genus, to pollination by birds.<sup>1</sup> We found this parasitic plant very commonly in the Bushveld and by no means confined to *Faurca*; indeed it was more conspicuous when on leafless trees such as Acacias, etc. Another common parasite was a mistletoe (*Viscum*) of very xerophytic structure (see fig. 2). It resembled closely *Viscum dichotomum*, being entirely devoid of assimilating leaves, while its nodes were flattened to take the place of leaves and each cladode-segment stood at right angles to the one above and below it.



Fig. 1.

Fig. 1. Foliage of *Faurca saligna* (Proteaceae).

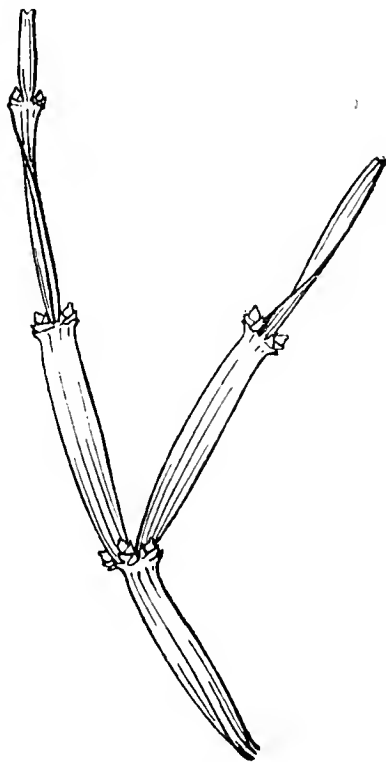


Fig. 2.

Fig. 2. A leafless form of mistletoe (*Viscum*) common in the Bush-veld.

The vegetation of the Bushveld was, as a whole, of less pronounced xerophytic habit than that of the high-veld, though occasionally one came across succulent tree-spurges on the hill sides and smaller succulent-leaved plants among the rocks. The grasses of the veld consisted largely of different species of *Aristida* (Twa grass) *Eragrostis* and *Andropogon*. The smaller herbaceous plants were in the Bushveld, as on the grass-veld, not very conspicuous during our visit, which took place at the end of the dry winter season. But in the moister region near the streams we

<sup>1</sup> See Maurice S. Evans. The fertilisation of *Loranthus Kraussianus* and *L. Dregei*. "Nature" Jan., 1895.

found purple flowered *Utricularias* and the white flower heads of *Kyllingia* (Cyperaceae), while in sheltered kloofs, *Aspidia*, *Osmunda* and *Cyathea Dregei* were abundant. Near Ottoshoop we came across a marsh and it was most interesting to note how closely the plants growing in it were related to those which would be found in a similar locality in England, while the rest of the vegetation of the district, xerophytic in character, was so little related to the British flora. Thus in the marsh we noted *Juncus*, *Hydrocotyle*, *Mentha*, *Phragmites*, and close to it a *Ranunculus*, while on the limestone ridge adjoining were succulent spurges, Aloes, Sanseverias and trees such as the Olive (*Olea verrucosa*) and Buffle-dorn or Hook and Stick thorn (*Ziziphus mucronata*, see Fig. 3).



Fig. 3. The Buffle-dorn (*Ziziphus mucronata*).

Like the Flora of Natal that of the Transvaal (included in the Kalahari Region of Bolus) seems very nearly allied to the great Tropical African Flora, but the greater rigour of the climate and the less abundant supply of water has made it less luxuriant, poorer in species, and also more xerophytic in character.

We have nothing in the Transvaal to compare with the luxuriance of forest vegetation of the Natal coast, but the grass-clad hills of Upper Natal are already reckoned to be Kalahari Region, and compare somewhat with the steppe-like vegetation of the High Veld. The Bushveld of the Northern Transvaal goes over

insensibly into the Central African Region, from which it has no doubt received the greater portion of its plants, while the presence of some Proteaceae such as *Protea* and *Faurca saligna* show that the somewhat more rigorous climatic conditions have preserved some forms of the older vegetation of South Africa, now for the most part surviving only in the south western Coast Region. The separation of these Proteaceous trees from the bulk of the older flora in the S.W. can be explained by the barrier caused by the excessively arid conditions of the intervening portion of the Kalahari and the Karroo regions, which cannot support a tree-like vegetation.

[NOTE.—I regret that I omitted to mention that the two photographs reproduced in Part I. were taken by my friend, Professor R. H. Yapp, who kindly allowed me to reproduce them. The Composite seen in the background of Fig. 1 of that Plate, turns out to be not *Helichrysum*, but *Metalsia*.]

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## RECENT WORK ON THE "REDUCTION DIVISION" IN PLANTS.

BY AGNES ROBERTSON.

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### I.—THE FACTS OF THE MATURATION DIVISIONS.

THE nuclear divisions which immediately precede spore formation in plants, and egg and sperm formation in animals, have been of late the subject of much controversy. In the higher plants the "spore mother-cell" (embryo-sac mother-cell or pollen mother-cell as the case may be) divides, and the two daughter-cells have nuclei with half the somatic number of chromosomes. This first division is called the *reduction division* or *heterotype* (Flemming). Each of the two cells thus produced divides again, and so four spores are formed characterised by possessing half the somatic number of chromosomes. This second division is called the *homotype* (Flemming). The reduced number of chromosomes appears at each of the succeeding divisions by which the gametophyte or sexual generation is produced, up to the formation of the egg and sperm cells. This reduction is clearly necessary in order to prevent the number of chromosomes increasing in geometrical progression in each generation. The question of exactly how the reduction is brought about has been answered in very different senses by different groups of observers. This answer is a matter of great importance from the point of view of theory, but we will defer for

the present the consideration of the *meaning* of the process and deal only with the observed facts.

With minor variations the accounts of the process lately published by the Louvain school<sup>1</sup> (Grégoire and his pupils) and the Bonn school<sup>2</sup> (Strasburger and his pupils), Charles Allen,<sup>3</sup> and H. O. Juel of Upsala,<sup>4</sup> shew a substantial agreement, and the views which they hold as to the actual sequence of events seem to be gaining ground at the present time. The view held by Farmer and Moore differs essentially from that of the observers just mentioned, and we will consider the main points of their description later, as well as the opinions of one or two other authors.

The Grégoire-Strasburger view, reduced to its simplest terms, may be epitomised as follows. In the mother-cell nucleus as it emerges from the resting state the chromosome substance collects into clumps, the number of clumps corresponding to the number of the somatic chromosomes. These clumps arrange themselves in pairs and then the whole chromosome-content of the nucleus contracts to one side of the nuclear cavity. During this contraction (known as "Synapsis") which is not artefact as has been sometimes supposed, but can be observed in fresh material,<sup>5</sup> the pairs of pro-chromosomes are brought into contact. Emerging from synapsis they elongate greatly, having joined more or less continuously end to end to form a double thread. The second contraction figure then sets in, during which the halves of the double spireme fuse to form a single thread. On emerging from this second synapsis the constituent threads again separate from one another. The double thread then segments into half as many lengths as there were somatic chromosomes, each of the definitive chromosomes so formed consisting of a pair of somatic chromosomes lying parallel side by side. In their 1905 publication Strasburger and his

<sup>1</sup> J. Berghs. "La Formation des Chromosomes Hétérotypiques dans la Sporogénèse Végétale." *La Cellule*, T. XXI, 1904 and XXII, 1905.

V. Grégoire. "La Réduction numérique des Chromosomes et les Cinèses de Maturation." *La Cellule*, T. XXI., 1904.

V. Grégoire "Les Résultats acquis sur les Cinèses de Maturation dans les deux Règnes." *Premier Mémoire. La Cellule*, T XXII., 1905.

<sup>2</sup> E. Strasburger, C. E. Allen, K. Miyake, and J. B. Overton. "Histologische Beiträge zur Vererbungsfrage." Leipzig, 1905.

<sup>3</sup> C. E. Allen. "Nuclear Division in the Pollen Mother-Cells of *Lilium canadense*." *Annals of Botany*, Vol. XIX., 1905.

<sup>4</sup> H. O. Juel. "Die Tetradenteilungen bei *Taraxacum* und anderen Cichorieen." *Kungl. Svenska. Vet. Akad. Handl.*, Bd. 39, 1905.

<sup>5</sup> E. Sargent. "The Formation of the Sexual Nuclei in *Lilium Martagon*." I. *Annals of Bot.* X., 1896, p. 451; II. *Ann. of Bot.* XI., 1897, p. 195.

colleagues have confined themselves to the description of events from the resting nucleus up to the formation of the definitive chromosomes. At this point the story is taken up by Professor Grégoire in his most recent paper, which deals both with animals and plants. By means of a critical investigation of the literature and many new observations he has traced the course of events with great clearness from the formation of the definitive chromosomes to the production of the spore tetrads. In plants the definitive chromosomes consist, as Strasburger says, of two limbs, and these are, according to Grégoire, parallel, crossed or interlaced, and present the form of a V, X, or Y. In certain plants the definitive chromosomes have been described as consisting at this point of four limbs instead of two, but Grégoire has shewn convincingly that at least in some of the examples usually quoted this is due to errors of observation. Grégoire uses the word "metaphase" for the period between the moment when the chromosomes first range themselves in the equatorial plane of the spindle, and the moment when the chromosomes destined for the two daughter nuclei lose contact with one another on their way to the poles. Nearly all botanists take the view that when the definitive chromosomes range themselves to form the equatorial plate at the beginning of the metaphase, they do not lie in the equatorial plane, but in a plane at right angles to this, so that one limb is orientated towards each pole, and in this position they become attached to the spindle fibres. This is called "insertion in superposition." The spindle fibres attach themselves to different points of the limbs of the chromosomes, so that these take the form of rods if the insertion is terminal, V's if it is median, and hooks if it is intermediate. On their way towards the poles during the "anaphase" (the period from the moment when the chromosomes destined for the two daughter-nuclei become quite free from one another, until the daughter-nuclei are completely formed) each of the limbs of the definitive chromosomes undergoes longitudinal fission. Each of the daughter chromosomes so formed will be one of the chromosomes for the four spore nuclei. The daughter nuclei do not pass into a state of complete rest, but their chromosomes undergo a varying degree of vacuolarisation and softening of outline which sometimes make them difficult to distinguish. In the second division (the so-called "homotype") there is no real fission of the chromosomes, since this has already taken place in the anaphase of the first division (the so-called "heterotype.")

We now pass on to consider how the description of the

reduction division published by Farmer and Moore<sup>1</sup> differs from that just given. These authors use the term "Maiosis" or "Maiotic Phase" to cover the whole series of nuclear changes included in the two divisions called "Heterotype" and "Homotype" by Flemming. They say that in the first synapsis a single thread is tangled up round the nucleoli. This thread then splits lengthways. The split closes again and the second contraction figure sets in, in which the thread shortens and thickens. The thread then disentangles and arranges itself into a number of loops. These loops next break apart from one another so that the nucleus contains a number of V-shaped structures in which traces of the longitudinal fission can still be detected. Each of these loops consists of two somatic chromosomes *united end to end*. The loops finally divide transversely at the apex, and one limb goes to each pole. On the way to the pole the original longitudinal split which occurred on emergence from the first synapsis reappears, and thus is formed the final number of chromosomes destined for the four spores. So Farmer and Moore agree with Strasburger and the Louvain School in supposing that the heterotype is a mechanism for sorting entire somatic chromosomes to the respective poles, but they disagree as to the method by which this is brought about. The main point on which they differ is that Strasburger thinks that the somatic chromosomes make their appearance *in parallel pairs* as soon as the mother-cell nucleus emerges from rest, and that the split spireme thread is formed by the end to end union of these pairs, whereas Farmer and Moore suppose that the somatic chromosomes unite *end to end*, and that it is the split arising in each of these somatic chromosomes which gives rise to the "split spireme." Thus the longitudinal split in the thread is interpreted by Strasburger as the re-separation of the pairs of somatic chromosomes which were originally separate but had fused, whereas Farmer and Moore regard it as the precocious appearance of the longitudinal split which will eventually in the homotype separate the daughter chromosomes for the spores. It should be mentioned that results agreeing with those of Farmer and Moore have been obtained by Lloyd Williams<sup>2</sup> for the Dictyotaceæ, and Gregory<sup>3</sup> for certain Ferns.

<sup>1</sup> J. B. Farmer and J. E. S. Moore. "On the Maiotic Phase (Reduction Division) in Animals and Plants." *Q. J. M. S.* Feb. 1905.

<sup>2</sup> J. Lloyd Williams. "Studies in the Dictyotaceæ," *Ann. of Bot.*, XVIII., 1904, p. 141.

<sup>3</sup> R. P. Gregory. "Spore Formation in Leptosporangiate Ferns." *Ann. of Bot.*, XVIII., 1904, p. 445.



Another group of observers (*e.g.* Miss Sargant<sup>1</sup>) have held the view that there is a *double longitudinal fission* of the originally single spireme. The appearance of parallel threads in the tangle emerging from synapsis, interpreted by Allen and others as the approximation in parallel of pairs of somatic chromosomes, and by Farmer as the folding together into a narrow loop of two somatic chromosomes united at one end, is by this school of observers regarded as the first longitudinal split in an originally single thread. A second split appearing in each half of the double thread, is interpreted as a precocious longitudinal fission, which will be completed in the homotype division.

The observers who take this view give us their facts but do not offer any suggestion as to how they are to be harmonised with what we know of the laws of inheritance. They are probably wise in this, since theoretical predispositions are particularly dangerous in cases where the actual observation is as difficult as it is here. Both Strasburger and Farmer on the other hand have laid much stress on the satisfactory relation which their descriptions of the process bear to certain widely accepted views on Heredity.<sup>2</sup>

## II.—THE MATURATION DIVISIONS AND HEREDITY.

It seems impossible to escape from the conclusion that it is the *nuclei* of the egg and sperm cells which carry on hereditary traits from one generation to another. This is now generally assumed as almost axiomatic. It is founded on the fact that fusion of one male and one female nucleus always occurs in fertilisation, whereas the behaviour of the cytoplasm is highly variable. Take the case for instance of two plants both belonging to the Coniferæ. "In *Taxodium* the whole male cell enters the egg; and the male cytoplasm forms a sheath round the fusion nucleus and takes part in the formation of the embryo, whereas in *Sequoia* the male nucleus slips from its cytoplasm and enters the egg naked."<sup>3</sup> If the nucleus is the physical basis of heredity the question next arises,—is any particular part of the nucleus definitely specialised for the function of "character-bearing"? The answer that at once suggests itself is that the chromosomes which reappear so definitely at each division are specialised for this purpose. But this is pure hypothesis. The care which is taken to distribute half of every chromosome to each

<sup>1</sup> E. Sargant. *l.c.*

<sup>2</sup> See also W. S. Sutton. "The Chromosomes in Heredity." *Biol. Bull.*, IV., 1903.

<sup>3</sup> A. Robertson. "Cytology and Classification." *NEW PHYT.*, Vol. IV., 1904. p. 138.

daughter-nucleus in typical cell-division, the very special mechanism for reducing the number of chromosomes during the maturation divisions, and the fact that as far as can be determined the sperm and egg nuclei at the time of fusion contain the same amount of chromatin, all strengthen the presumption that with the chromosomes is associated the power of transmitting hereditary characters from one generation to another.

Some support for the view that the chromosomes retain their individuality during the resting period is afforded by the fact that immediately before division they are often orientated about a pole, corresponding in position to the pole towards which in the previous division the chromosomes of the daughter nucleus passed.<sup>1</sup> If the chromosomes really retain their individuality, however often the nucleus divides, and if, further, there is *not* at fertilisation (as recent work seems to suggest) any actual fusion of chromosomes, it follows that the chromosomes derived from the male and female parent must exist side by side in the nucleus throughout the development of the plant! 'Blackman<sup>2</sup> says "all the cytological work of recent years tends to show that the chromosomes have a distinct 'individuality,' and the nuclei of the cells of the higher animals and the nuclei of the sporophytic cells of the higher plants are really *dual* in nature, there being no real mixing of the chromatin from the two sources until the time of chromosome-reduction." There is a certain amount of evidence to shew that at least in some cases not only do the chromosomes retain their individuality throughout the development, but the whole male and female spiremes exist, at least for a time, separately in the fusion nucleus and the nuclei resulting from its divisions. Miss Ferguson<sup>3</sup> has shewn that in *Pinus strobus* two separate spiremes can be recognised in the third division of the egg. Strasburger however will not allow that there is any reason to suppose that in ordinary plants the male and female *spiremes* persist separately throughout the sporophyte. He refers to the remarkable case of the 'Uredineæ'<sup>4</sup> where a process occurs which is apparently an extremely reduced form of fertilisation. An ordinary vegetative cell in the tissue close to the female cell functions as the male cell, and its nucleus enters the female cell. The two nuclei do not fuse, but persist separately through the

<sup>1</sup> E. Strasburger. l.c.

<sup>2</sup> V. H. Blackman. "On the Fertilisation, Alternation of Generations, and General Cytology of the Uredineæ," *Annals of Botany*, Vol. XVIII., 1904.

<sup>3</sup> M. C. Ferguson. *Proc. Wash. Acad. Sci.*, Vol. VI., 1904.

<sup>4</sup> V. H. Blackman. l.c.

“sporophyte.” Strasburger regards the special case of definite duality in the “sporophyte” nuclei as due to the fact that the nuclei being derived from neighbouring cells are too closely related to attract one another strongly.

According to the most recent views of the Louvain and Bonn Schools, as we have shewn in the first section of this article, the full number of somatic chromosomes before the reduction division emerge from the reticulum of the resting nucleus, as they do also before a vegetative division. But their arrangement differs from that characteristic of a vegetative division in that they are grouped in pairs, and at the division one of each pair goes off to each daughter nucleus. The view which Strasburger holds is that these pairs of chromosomes owe their origin to the preceding fertilisation, and that one is derived from the male parent and one from the female parent, and further that they do not come together accidentally, but that “homologous” chromosomes seek one another out. If each chromosome is responsible for the transmission of a certain number of hereditary qualities we should suppose, for instance, that if the plant whose reduction division we are considering was a hybrid made by crossing a green-seeded pea with pollen from a pea of a pure yellow-seeded race, there would be a certain pair of homologous chromosomes present, both bearing the character of seed colour, one of which came from the male parent and bears the quality of yellowness, and the other from the female parent and bears the quality of greenness. In the reduction division the two members of this pair of homologous chromosomes would go off into the two daughter nuclei. In the succeeding homotype division each chromosome would split lengthways into two equivalent halves, one of which would go to each spore, so that eventually two of the four spores would have chromosomes bearing the quality of “green seededness,” and two, the quality of “yellow-seededness.” This conception is of course purely hypothetical, and we can have no rigid demonstration of its truth. But it is at least a good working hypothesis, enabling us to harmonise the observed facts of cytology with the idea of the “purity” of the germ cells with respect to certain allelomorphic characters deduced from the experimental hybridisation work of Mendel and his followers.<sup>1</sup> If we suppose that each chromosome bears a number of hereditary qualities, and that it is a matter of chance towards which pole the male and female members of each homologous pair move off, we see that

<sup>1</sup> R. C. Punnett. “Mendelism,” Macmillan and Bowes, 1905.

<sup>2</sup> C. Allen. *l.c.*

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considering the number of chromosomes many plants possess, the number of possible combinations of characters transmitted by the germ cells must be exceedingly great. Probably, too, the chromosomes themselves are very elaborate structures. "The smallest visible chromative granules may themselves well possess an inconceivably complex structure; and it is not yet practicable to attempt to identify the lowest observable order of elements in the spirem-thread as the bearers of the apparently simple unit qualities manifested by the organism." Strasburger thinks that the yellowness or greenness of the yellow or green pea depends on a single "pangene" (one of the ultimate units of which the chromosomes are built up) but he considers it unlikely that the sole task of any pangene would be to determine the colour of the cotyledons, and is inclined to think that from each such pangene in the course of development of the organism a whole series of impulses would arise. The idea that certain definite pangenes are always associated together in one chromosome enables us to form a reasonable mental picture of a physical basis for "correlation" of apparently unrelated characters.

Wager,<sup>1</sup> who lays great stress on the function of the nucleolus in storing chromatin and supplying it to the chromosomes, claims that the nucleolus must be considered in any future attempt to discover a cytological basis for the laws of heredity. But this seems to me to be founded on a misconception. When we speak of the "individuality" of the chromosomes, their "permanence," and the presence in them of definite pangenes determining certain characters, we do not of course mean that the chromosome is a stationary structure which persists as such throughout the life of the plant. It is clearly *not* so, for in the resting nucleus it is no longer visible in its characteristic condensed rod-like form. The thing that we conceive of as really permanent, in the sense that it is able to reproduce itself in each division, is the arrangement of the ultimate particles in each chromosome, and their relation to one another. Any given homologous pair of chromosomes appearing in the reduction division is "identical" with the corresponding chromosomes occurring in the previous egg and sperm nuclei only in the sense in which we use the word when we say that our present day selves are identical with ourselves of ten years ago. We feel a moral conviction that our identity is carried

<sup>1</sup> H. Wager. "The Nucleolus and Nuclear Division in the Root-Apex of *Phaseolus*." *Annals of Bot.* 1904.

on though we no longer consist of the same material particles, and in the same way the chromosome may retain its individuality though it has at one time been fed by chromatin from the nucleolus, and at another time given up its chromatin to the nucleolus.

It is quite true that "le dernier mot n'est pas encore dit sur la question de l'hérédité, la question de la réduction, de l'essence des divisions sexuelles, ni même sur la nature de la cinèse somatique,"<sup>1</sup> but still I think we may say of the most recent view which is in essentials common to the Louvain and Bonn schools, "Se non è vero, è bene trovato."

<sup>1</sup> F. A. Janssens. "La spermatogénèse chez les Tritons." *La Cellule*, T. XIX. 1901.

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## NOTES ON CEREALS.

BY ERIC DRABBLE.

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Through the kindness of Messrs. Gartons, Ltd., of Warrington, I have recently had the opportunity of examining very fully their methods of producing new breeds of Cereals on their experimental farm at Aeton Grange, in Cheshire. A full account of their methods and results will be published elsewhere, but several points of general botanical interest have been noticed in the course of the work, and a short account of these is given below.

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### METHODS EMPLOYED IN PRODUCING NEW BREEDS.

Wheat, Oats and Barley have all been used experimentally. Races already possessing desirable qualities, in many cases combined with less desirable or even undesirable characters have been chosen as parents. Crosses have been made by removing the anthers of the female parent at an early stage, and applying to the stigma pollen from the male parent. It is necessary to remove the stamens at a very early stage indeed, as it appears that the cereals are normally self-pollinated before the pales open. It is certain that the unopened flower shows the presence of pollen upon its stigmatic lobes. When the stamens protrude they appear at first sight to be entire, but careful examination shows that a partial dehiscence has already taken place, and through this the pollen grains found on the stigma have come. Hence it is evident that the stamens must be removed carefully before such dehiscence has taken place. The pales are opened with forceps, the stamens removed, pollen from

the male parent is applied to the stigma, and the pales are again closed.

The process of events in the flower previously to, and during pollination, is as follows. Before self-pollination has occurred the stigmas converge. The anthers then partially dehisce, and pollen is shed on to the stigmas while still enclosed within the pales. Immediately after this pollination the stigmas diverge and emerge laterally from between the pales. Now it is that cross-pollination may take place, though according to Mr. Garton's results, cross-fertilization would appear to supervene but rarely. A few hours after the emergence of the stigmas they again converge, and this is accompanied by a general contraction of the stigmatic lobes.

The evidence for self-pollination is strong, though this does not necessarily involve the absence of later cross-pollination, which may indeed be prepotent, but in no case has Mr. Garton been able to produce a hybrid by application of pollen from a male parent to the extruded stigma of the female—the pollen must be applied to the stigma before it extrudes.

The fruits of the flowers thus cross-pollinated are allowed to ripen, and are gathered and kept separately. They are sown next season, and *all* the grain from each plant is kept separately. This is sown in rows the following season, the produce of each plant having a row to itself. The resulting plants are found to show great sporting; some being superior in certain characters to the parents, others being inferior. The plants which in the characters desired are found to be the best are noted, and the grain is kept and sown the following season. Again the resulting plants will show a tendency to sport, but less markedly so than in the last season. The best are again selected and the grains sown, and a further selection is made, until finally a progeny is obtained in which the sporting is slight and almost negligible. The race is then said to be *fixed*. By this is meant that so long as the plants are allowed to breed naturally, as Mr. Garton believes entirely by self-fertilization, no further sporting will occur.

#### COMPOSITE CROSSES.

Many races may be combined in the production of new breeds. As an example may be cited the ancestry of the breed "New Era." The wheat known as "Talavera" was crossed with a form of *Triticum spelta*, and the progeny which we may call  $\alpha$  was raised. At the same time the wheat "Bartweigen" was crossed with "Fultz," and again the progeny was raised ( $\beta$ ).  $\alpha$  was then crossed with  $\beta$  and

repeated selection of the most desirable forms resulted in the establishment of the new race "New Era."

It may sometimes be desired to introduce into a hybrid characters possessed by two forms which will not readily cross, or which will not produce fertile offspring. In such a case each form is crossed with some other form for which it has "affinity," as the breeders express it, and the resulting offspring are then mated. This will in many cases lead to a progeny, some members of which possess the desired characters.

Or suppose again that four varieties are crossed in pairs; the progeny of each is fixed and a cross between them is instituted, and suppose that some of the offspring show characters which it is desired to fix at once, although the progeny as a whole is sporting, and will continue to sport for several generations. The desirable plants are each crossed back with one of the parents. In this way a fixation of the required characters in some of the progeny takes place quickly. This is of considerable interest and can be co-ordinated with certain facts of cytology.

The members of the fixed type may deteriorate after several generations although they do not change their characters. Cross-pollination amongst themselves will bring them back to their former vigour without causing undue sporting. A slight tendency to sporting may be induced, but not sufficient to materially change the race. It is of very great interest, however, to note that if the forms crossed have been grown under *different conditions*, although their ancestry has been the same, the sporting induced is greater than if they had been grown under exactly similar conditions.

#### SOME RESULTS OF COMPOSITE CROSSING.

A great defect of all cultivated wheats with the exception of *T. turgidum* and *T. spelta* is that the grain tends to drop out when ripe. A serious drawback to these two forms of wheat, however, is that the rachis breaks up, so that on threshing, the spikelets are separated, each attached to a portion of the rachis. By crossing any of the cultivated forms of *T. sativum* with a spelt wheat, varieties may be fixed which retain the grain but are without the property of breaking up. A breed has been produced which will retain its grain for four weeks. This is of great importance for large grain-growing countries where the whole of the crop must be harvested within the period between ripening and shedding of the grain. In Australia, where the grain is harvested by the stripper

which threshes the wheat in the process of harvesting, such breeds are useless.

One of the peculiarities often shown by the products of composite crosses is that the spikelets instead of producing the normal number of grains—about six—become elongated and carry as many as fourteen grains. In certain cases the whole head becomes vegetative and the pales grow out as foliage leaves—four inches or more in length.

#### BARLEY.

In the Barleys on each side of the rachis are rows of spikelets. These spikelets are in sets of three, a central one, and two lateral ones. In the two-rowed barleys only the central spikelet of each triplet produces grain, and hence there is a single row of grains on each side of the rachis. In the six-rowed forms all the spikelets produce grain, leading to the development of three rows of grain on each side. By crossing two- and six-rowed varieties, all forms are found in the offspring from the development of grain in the central spikelet on each side only, to the development of grain by all three spikelets; also forms occur in which the normally fertile central spikelet becomes barren and only the lateral ones are fertile. This leads to a four-rowed barley—the only truly four-rowed form known, the so-called four-rowed barleys of commerce being only irregular forms of the six-rowed types. A point of some interest is found in connection with these hybrid barleys. In the earlier generations of many of these six-rowed hybrids, the lateral grains are very much smaller than the central ones—that is they contain much less endosperm. But by collecting the small lateral grains and growing them separately the progeny is as vigorous vegetatively and reproductively, and gives as great a percentage of germinating grains as the progeny from the large central grains. Indeed, cultivation has led to the development of more endosperm in the grain than is necessary for the nutriment of the young plant.

A *hulled* barley is one in which the pales adhere to the ripe grain. In a *hull-less* barley the grains are free. In the hulled forms the stamens though detached at the base are not completely thrown out, but are held by the pales. They seem to serve as a point of attack for fungal parasites, the mycelium then invading the grain. In hull-less forms the danger is obviated as the anthers are completely shed. In the hulled varieties the style also persists and seems to serve as a second point of fungal attack. All forms found



in the hulled varieties have been produced also by appropriate composite crossing in the hull-less forms also.

There are certain varieties of barley in which the awns fall off on ripening. These are termed beardless barleys. When the beard falls off, the apex of the grain is exposed to the attacks of fungi. In the long-bearded forms which return their awns there is danger of interlocking of the awns and consequent levering off of the grains. An attempt is now being made by Mr. Garton to produce *shortly* awned varieties with the best quality of grain.

Plants in the sporting stage are more susceptible to fungal attacks than are the fixed breeds.

Crossing different breeds of barley leads to practically no sterility. In wheats the crossing of extreme forms introduces some lessening of the fertility, and in oats it often leads to a considerable degree of sterility.

#### OATS.

Dull weather at the time of pollination in Oats may lead to a loss of 25% in the yield of the crop. Such sterility is generally to be traced to the inactivity of the pollen grains.

The wild *Avena fatua*, however, produces fertile anthers and active pollen grains even in very dull weather. This plant is extremely fertile in the wild state, most of the flowers producing grain. It has been extensively used at Acton Grange as a parent in composite crossing, since it leads to the production of a larger percentage of flowers with fertile anthers and also to a greater yield of grain.

In the Oat-spikelet the lower grains are larger than the upper ones. These two forms have been collected and sown separately. The resulting crop shows that the smaller ones are as fertile in every way as the larger ones, and that in the latter the young plant attains its independence long before the whole supply of endosperm has been absorbed. In *Avena fatua*, however, practically all the endosperm is required.

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## INCIPIENT VITALITY.

[An account of some recent work throwing light upon the Chemical Mechanism of the Cell.]

BY F. F. BLACKMAN.

THIS article is intended to supplement one entitled "Residual Vitality" which appeared in this Journal two years ago.<sup>1</sup> In the former article attention was drawn to the evidence that vitality is not the property of a single chemical substance, protoplasm, but is the attribute of a *system* of correlated substances, which substances in themselves may be, in comparison with the whole system, quite simple in composition and attributes. It was shewn that a number of these units may be liberated by destruction of the system, even, under appropriate conditions, by the crude method of physical disintegration. A number of them have been grouped into one class, the enzymes, not because they produce the same sort of effects chemically, but because they all act in the same sort of way, as *katalytic agents*. It was further shown that the vital system must be a compound one, consisting of simple systems aggregated into more complex ones to several degrees, giving, as a result, a gradation of functions the higher of which may be suppressed without suspending the lower, while the lower cannot be stopped without suspending all the higher. As stages in such a sequence of functional manifestations, proceeding downwards, we may particularise—irritability, growth, anabolism, respiration, enzyme-action.

In death, by natural or artificial process, these functions often fail in sequence from above downwards, and if the progression is slow we have stages where the lower grades of the vital manifestations alone co-exist. Such states, when they are maintained long enough to be experimentally demonstrable, may be entitled residual vitality and they gave title to the earlier article.

At that time the point of view was purely analytical, dealing with the breaking down of the full manifestations of vitality and with the residual fragments so obtained.

Now, there is enough analytical knowledge available to justify a first tentative attempt at synthetic treatment, and we may begin to speculate as to how the metabolic processes of the cell are adjusted as regards the *rate* at which they take place in life.

The clues to this enquiry must be sought in the chemistry of the non-living, and the investigator must dare to ask why does not

<sup>1</sup> NEW PHYTOLOGIST, Vol. III., Feb. 1904.

that which takes place in the test-tube take place also in the cell.

It is very interesting to note that the desired *rapprochement* between the test-tube and the cell is not all the work of the biologist who craves for it, but is largely the work of the less emotional chemist. With the growth of the science of Physical Chemistry a change has come over the chemist's point of view bringing it much more that is everywhere realised into line with that of the biologist.

Until this change of view, an equation in terms of molecules represented the goal of the chemical investigation of a reaction. Now, the successive stages or development of the chemical change, the energy-change involved in it, and the *rate* at which it progresses<sup>1</sup> are the subject of exact investigation; while more biologically still, a study is made of the conditions under which it occurs and of the effect upon it of variation of external conditions (temperature, light, etc.) and of the effect of the presence of other material substances (such as solvents and katalytic agents) upon its rate or nature.<sup>2</sup> Here we have a close historical parallel with the primary lines on which the physiological phenomena of the living plant have been investigated.

Let us consider a single simple reaction. The chemist is no longer satisfied with knowing that  $2\text{H}_2 + \text{O}_2 = 2\text{H}_2\text{O}$ , but the temperature conditions required to bring this change about are determined. In a glass vessel the gases must be heated to  $448^\circ\text{C}$  before there is any formation of water: in a silver lined vessel  $182^\circ\text{C}$  is sufficient: in contact with finely divided Platinum-black, union begins at  $50^\circ\text{C}$ , while in the presence of colloidal Platinum<sup>3</sup> the union is vigorous at the ordinary air-temperature. All these agents which, by their presence, cause the reaction to go on more quickly than it otherwise would, are called katalytic agents. They are not destroyed by their activity, so a trace of them will in time

<sup>1</sup> Most reactions that the student of chemistry has to deal with take place so quickly, when the reacting bodies are once mixed, that they may be regarded as instantaneous. Many organic reactions, as those of hydrolysis, saponification, and fermentation take place at a very slow rate which can easily be exactly measured. All the important metabolic chemical changes of living cells appear to be essentially slow reactions.

<sup>2</sup> See for example, Mellor, *Chemical Statics and Dynamics*, 1904, pp. 1 and 2.

<sup>3</sup> This is metallic Platinum in a very fine "ultramicroscopical" state of division. It is produced as a permanent suspension in water by electrolysis of solutions of certain salts of Platinum. It appears perfectly homogeneous and clear to the eye, but lacks all the characters of a true solution. Bredig, *Anorganische Fermente*, Leipzig, 1901.

produce an enormous effect. The best theory of their action is that they form intermediate compounds with the substances to be changed. Thus the Pt. first unites with the  $O_2$  and the oxide then reacts with the  $H_2$  to form water, regenerating the Pt. For the Pt. to have this accelerating katalytic action it must happen that Pt. reacts quicker with  $O_2$  and the oxide reacts quicker with  $H_2$  than oxygen would unite directly with hydrogen. Of course a katalyst cannot supply energy, and no energy is required to unite  $H_2$  and  $O_2$ , but on the contrary latent energy is liberated, so that the katalytic agent has quite an easy and almost accidental function which it can continue indefinitely.

In thus accelerating the reaction the katalyst produces just the same effect as an increase of temperature would. Striking as it is to see hydrogen and oxygen uniting rapidly at the ordinary temperature instead of requiring  $500^\circ C$ , yet there is nothing mysterious about it, and it is only that a naturally slow reaction is enabled to go on as fast as do so many ordinary reactions (say  $HCl$  on  $Na_2CO_3$ ) without any intervening katalytic substance.

Now it is instructive to recall that this power of carrying on at low temperatures reactions which require a high temperature to go by themselves, has long been regarded as the mysterious prerogative of protoplasm. The explanation is then clearly this, that protoplasm is a complicated congeries of katalytic agents, adapted to the metabolic work that the cell has to do.

These protoplasmic katalysts are grouped together as enzymes. They are indiffusible colloids, probably proteid in nature, of varying degrees of simplicity and stability and either naturally free in the *reticula* of the protoplasm or forming hypothetical "enzyme-branches of the protoplasm." Every year new ones are isolated, and it would seem that there may well be one for every change the cell conducts that is not naturally capable of proceeding rapidly at the vital temperatures.

In 1897 Buchner, by the quite new method of expressing the liquid contents from living cells, succeeded in preparing the katalytic agent (zymase) of the last outstanding fermentation-process, the alcoholic fermentation of sugar by yeast. Thus was swept away a vitalistic barrier that many thought would last for all time and a large region of vitality has become the "Hinterland" of pure chemistry.

Progress along Buchner's lines soon showed that it was not necessary to break up the yeast-cells in order to get alcoholic

fermentation apart from their vitality. In 1901, Albert<sup>1</sup> discovered that yeast retains the power of fermenting sugar after it has been killed by treatment with a mixture of alcohol and ether. A yellowish powder is thus obtained consisting only of killed cells which contain the whole of their zymase precipitated within them. Such killed yeast was much more efficient than Buchner's pressed out sap; it is quite easily prepared and has been used commercially. The colloidal proteid enzyme, zymase, which effects the fermentation, does not diffuse out of the cell into the surrounding water even when the protoplasm is thus killed, and so an active *extract* can no more be prepared from these killed cells than from living ones until they have been broken up. It follows that the sugar molecules of the medium must still diffuse into the cells, before they can be split up. Accurate comparison has not yet been made between the activity of the same cells living and killed, but the latter are at first extremely efficient. If the activity of these killed cells did not, after a time, disappear they would be a perfect substitute for living cells. We have to enquire how it is that their activity steadily diminishes, for it is a characteristic of enzyme katalytic action that the agent is not destroyed by its action.

Albert showed that a number of other enzymes were at work in these killed cells carrying on the same processes as occur in the living cell. Among these was an active proteolytic enzyme that causes the dwindling of the proteid granules which are conspicuous in the freshly killed cell (staining blue with Gram's stain). The products of the action of this enzyme, and later the enzyme itself, diffuse out of the cell and finally the proteids are all broken down to leucin and tyrosin. The disappearance of the sugar-fermenting power after some twenty hours of activity is attributed by Albert to the action of this proteolytic enzyme which actually digests the proteid particles of the sugar-splitting enzyme. Were it possible to destroy or inhibit the proteid enzyme first, then the sugar fermentation would be more permanent.

Invertase, the enzyme which inverts cane-sugar to glucose and levulose, is also active in the killed yeast. This is generally considered to be the simplest of the enzymes and, in agreement with this view, it is found that it diffuses very quickly out of the dead cells and is at work in the solution.

There is also present a glycogen-fermenting enzyme which acts

<sup>1</sup> Albert, Ber. chem. Ges., XXXIII., 1901, and Centrbl. f. Bakt., VII., 1901.

on this carbohydrate reserve of the cells giving rise to alcohol and  $\text{CO}_2$  in small quantities even in the absence of added sugar. As regards this process Albert has shown that neither the glycogen nor the enzyme can diffuse at all out of the dead protoplast. In addition there are no doubt other enzymes at work in these killed cells, accelerating other metabolic changes just as in life.

Though these cells have no power of budding or growing or, presumably, of increasing their substance, they can still hardly be called quite dead with so much of their metabolic machinery still functioning, and German writers distinguish this condition as "abgetöteten" (killed) as opposed to "abgestorben" (dead of a natural death).

A very similar state of things has been described by Beijerinck<sup>1</sup> for the *Urococcus* which converts urea into ammonium carbonate. The change is attributed to an enzyme, urease, which continues to function after the bacteria have been killed with alcohol. Here also the enzyme does not diffuse out of the cell, killed or alive.

More recently Stoklasa<sup>2</sup> has shown that the characteristic enzyme of yeast, zymase, also occurs in the cells of the higher plants, perhaps universally. It can be separated and made to ferment sugar *in vitro* by expressing the sap from the fresh parts by a pressure of 300 atmospheres. This extract is then precipitated with a mixture of alcohol and ether. The precipitate is quickly dried *in vacuo* and then keeps well. Whenever it is added to a sterile solution of glucose, active formation of alcohol and carbon dioxide at once takes place and lasts for a varying number of days.

It has long been known that when the higher plants are kept deprived of oxygen, they produce alcohol and  $\text{CO}_2$ , just as yeast does, but the process here has the special name of intra-molecular respiration. It is now clear that in both cases we have a splitting up of sugar by the same enzyme, zymase.

Godlewski<sup>3</sup> has further shown that intact Lupine seeds will, during their germination, cause the splitting of glucose when kept, quite sterile, submerged in a sugar-solution in the complete absence of oxygen. Not only do the scanty carbohydrate reserves of the seeds disappear but the sugar from outside is acted upon by the zymase of the seeds, and alcohol and  $\text{CO}_2$  are formed in the calculated proportions.

<sup>1</sup> Centrbl. f. Bakt. VII., 1901.

<sup>2</sup> Ber. deut. chem. Ges. XXXVI., 1. Jan. 1903, Centrbl. f. Bakt. XIII. 1904, Pflüger's Archiv. CI., 1904, etc., etc.

<sup>3</sup> Bull. Acad. Sciences, Cracovie, March, 1904.

The burning question of the hour is whether this universal zymase really contributes the first stage of normal respiration; whether, in the presence of oxygen also, sugar is normally split up to form alcohol and a certain amount of  $\text{CO}_2$ , after which the alcohol is then further oxidised to water and more  $\text{CO}_2$ . The latter stage would be presumably accelerated by an oxidising enzyme, an oxydase, and naturally would be suspended in the absence of available oxygen. Various oxydases are present in living cells, but no evidence of one accelerating the oxidation of alcohol has yet been obtained.

The most recent contribution to this line of work has been made by Palladin.<sup>1</sup> He has made two important advances. He has shown that massive organs of the higher plants can be killed without destroying their various enzymes by the action of sudden intense cold, and that onion bulbs, for instance, on thawing after a short exposure to  $-20^\circ\text{C}$ , give out  $\text{CO}_2$  for a period of many hours. This is due to the action of the same enzyme that works in yeast. This freezing method is much more suitable for dense impervious plant-organs than the use of alcohol and ether.

Palladin has further shown that, with some plants, the enzyme does not come out into the expressed sap, but remains behind in the residue, either because it is insoluble or, perhaps, is still part of the protoplasmic complex. Experimenting with the whole organ after freezing gets over this difficulty, and one is enabled to determine the  $\text{CO}_2$  output of the same organs before and after this killing.

Palladin makes the interesting observation that the heightened respiration during life, produced by ether or quinine, has no persistent effect in the way of increased  $\text{CO}_2$ -output from the enzymes of the part after freezing. From this he concludes that the  $\text{CO}_2$  of respiration has at least a double origin, part coming from enzyme activity, and a part, which he calls "Reiz- $\text{CO}_2$ " (stimulus- $\text{CO}_2$ ), coming from the protoplasm itself as a result of the stimulus of the ether or quinine; the latter part disappears on killing the protoplasm. So also the immediate increased output of  $\text{CO}_2$  on wounding bulbs has no counterpart in the  $\text{CO}_2$ -output after freezing, being "Reiz- $\text{CO}_2$ ," while the reparative processes that set in several days after wounding lead to an increase of tissue protoplasm and of enzymes, and so produce an increase in the  $\text{CO}_2$ -output, as compared with an uninjured control; and this persists after killing.

<sup>1</sup> Ber. deut. bot. Ges. XXIII., July, 1905.

Present among the enzymes of these organs killed by freezing is also an oxydase enzyme which causes  $\text{CO}_2$  to be given off when hydrogen peroxide is added to the extract. This effect is destroyed by heating the extract, and so is due directly to the oxydase; this makes a third category of  $\text{CO}_2$  production, "oxydase  $\text{CO}_2$ ."

A recent paper by Chodat and Bach<sup>1</sup> provides a direct proof that an oxydase enzyme is actually at work in the living cell. One of the characteristic properties of such oxidising ferments is that of decomposing hydrogen iodide with the liberation of Iodine. If a drop of plant-extract containing oxydase be placed upon starch-paper, which has been dipped in KI and dilute  $\text{H}_2\text{SO}_4$  and then dried, a blue spot is formed, due to the union of the liberated Iodine with the starch. It is now shown that exactly the same reaction can be brought about in the living cell. The cells of the peripheral part of a potato give an active oxydase extract; they contain starch and their sap is acid. If then KI could be introduced into the living protoplasm the starch should stain blue. When a thick section of potato is placed in dilute KI the cells are plasmolysed, but some of the iodide enters the protoplasm, and the starch actually does turn blue. That the protoplasm is not killed is shown by the fact that the cell recovers its turgor when placed in pure water.

As further evidence it is shown that when pyrogallol diffuses into these same living cells, a reddish crystalline precipitate of its oxidation-product, purpurogalline, is quickly formed.

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There is thus a steady accumulation of evidence that each chemical change in the living cell is fostered and accelerated by a special enzyme. It is further now proved that these enzymes work efficiently after the cell is killed, and that their action is in no way vitalistic, but of a purely chemical katalytic nature. We may, then, turn now to consider what light physical chemistry can throw upon the mechanism by which the *rate* of enzyme activity is determined in the cell and maintained usually at a suitable biological intensity.

Except for the presence of katalytic enzymes the various metabolic single changes would be too slow for biological continuity. On the other hand, when accelerated by katalytic agents, they might easily go wastefully or even injuriously fast. This

<sup>1</sup> Archives des Sciences physiques et naturelles, t. XVII., May, 1904, p. 484.



however, is not what one expects or finds in the plant at temperatures of which it has had previous experience. How then is regulation attained? This is the first step to be considered in building up a synthetic conception of cell-activity from the known activity of its isolated enzymes.

The biological study of chemical reactions by the physical chemist has shown that *temperature* and *mass* are the two primary factors that control the rate of reactions in the test-tube. All reactions are accelerated by a higher temperature, and the acceleration is generally approximately uniform. For the sort of reactions that take place in the cell, the rapidity of the change is doubled or trebled for each rise of  $10^{\circ}\text{C}$ . Now we find in the higher animals that the temperature of the body is very carefully kept at a uniform level, which is much above that of the environment. Of course the heat needed has to be generated by certain special metabolic changes, but there is a uniform high rate of general metabolism attained in this way, and the system is thus free to adjust itself to various other calls upon it. The higher plants are very different from this, and are entirely subject to external temperatures. They must therefore survive wide ranges of temperature variation naturally, and they can resist still wider ranges experimentally. There is no evidence that they seek to compensate the direct physico-chemical effects of temperature changes by regulatory process, but the plant has hardly been investigated critically from this point of view. It is true that a leaf in direct sunshine cools itself by the evaporation of water, but this seems to be of secondary significance.

One must not think that plant-cells are fundamentally so sluggish that the higher activity conditioned by a high body-temperature is impossible for them. Does not the *Arum* spadix raise its temperature up to even  $50^{\circ}\text{C}$ , and some  $34^{\circ}\text{C}$  above its environment by the local activity of its metabolism? Does not the stalk of the sporogonium in *Pellia* grow from a length of two millimetres to eighty millimetres in three or four days? Yet the plant submits to have its metabolism varied with every passing change of external temperature. Nevertheless it distinguishes itself from the inert masses around it by regulation of its metabolism, for such is the essential of life, but not by regulation by means of temperature.

A consideration of other methods of regulation brings us to some discussion of the influence of *mass* on the rate of chemical

change in the test-tube and in the cell. The law of mass-action states that the amount of chemical action going on at any moment at a given spot is proportional to the quantity or mass of the reacting substances that are present. Katalytic agents naturally obey this law; if a double amount of enzyme is present in a solution it converts twice as much substance in a given time as a single amount would. Now, even with the acceleration produced by a katalytic enzyme all ferment actions are slow and if a reaction is started with a definite amount, say, of invertase, and a definite amount of cane-sugar in a beaker, it is many hours before all the sugar is "inverted." The inversion of the sugar is at first fast, and so the amount of the sugar rapidly decreases; from this it follows by the law of mass that the rate of inversion will now fall off also, and so it does, tailing off more and more as the amount of sugar becomes diminished.

If *half* the total sugar be inverted in the first hour, then  $\frac{1}{2}$  the remainder ( $=\frac{1}{4}$ ) will be inverted in the second hour,  $\frac{1}{2}$  the new remainder ( $=\frac{1}{8}$ ), in the third hour,  $\frac{1}{4}$  in the fourth hour, and so on never reaching absolute completion in theory, but coming near enough to it in practice. This march of the conversion can be graphically represented from these data by a regular falling "logarithmic" curve showing the rate of inversion at any moment.

From analogy with the action of colloidal Platinum as a katalytic agent, it is held that the enzyme unites temporarily with the sugar molecule, and the water molecule, and that this so-called "active system" at once splits up, regenerating the enzyme and leaving the sugar so acted upon by the water that it is inverted from cane-sugar to glucose and levulose. The rate of the compound process of inversion must depend upon the rate of formation of the "active system" and the rate at which it splits up again. The amount of enzyme in the solution remains by definition unchanged, so that the rate will come to depend only upon the amount of cane-sugar present. A constant fraction of the total number of sugar molecules present (50% per hour in this assumed case) unites with enzyme to form the active system. Here the enzyme is assumed in excess, and the sugar is the limiting factor to the rate of inversion.

One can however for a time produce a different balance of activity in the solution. Suppose that at the beginning, cane-sugar molecules are very abundant and enzyme particles are very few. Then the number of active systems formed (in the hour) will be limited by the scarce enzyme and many of the sugar molecules will

not come across the enzyme at all in their wanderings. Now as long as the sugar remains in excess, the number of active systems formed and broken up again per hour will remain *constant* because the enzyme particles do not become reduced in number by their activity. For a time then in this case the absolute *rate of inversion will remain uniform* (and graphically representable by a straight line) hour after hour, and only when the cane sugar is inverted to such an extent that the number of sugar molecules and not the number of enzyme particles becomes the limiting factor, shall we get the falling regular logarithmic curve that we spoke of before. This state of things is quite easy to produce in the test-tube. It has been observed by Horace Brown and Glendinning with Diastase; and fully explained by E. F. Armstrong in his *Studies on Enzyme Action*.<sup>1</sup>

It is of very great interest to the writer that this state holds also in the living cell under conditions that may now be briefly explained. A cut leaf that has been assimilating, contains a certain amount of sugar, the fate of which it is to be burned up in respiration. If such a freshly cut leaf be kept in the dark at a constant temperature and its respiration be measured continuously it will be found that for a number of hours the  $\text{CO}_2$  production remains uniform, and that subsequently, when the sugar supply is so reduced that it becomes a limiting factor, a uniformly falling rate of respiration sets in. This fall continues until all the available sugar is consumed and the respiration of the starving leaf exhibits a regular falling logarithmic curve, lasting for perhaps ten days and exactly like the curve obtained with the action of an isolated enzyme in a test-tube.

We have exhibited, here then, a pure mass effect in the living cell. In accordance with expectation, we find that with starving leaves at a higher temperature, containing the same initial amount of sugar, the respiration begins at a higher level, and therefore reduces the stock of sugar faster. As a consequence the initial period of uniform rate is proportionately shorter and the falling curve sets in sooner, but then follows the same course as with the leaves at a lower temperature. If at any time after the respiration has begun to fall off, fresh sugar be supplied to the cells of the leaves by putting them in the light with  $\text{CO}_2$ , then the respiration goes up again. If enough sugar has thus been given, the respiration

<sup>1</sup> Proc. Royal Society, Vols. 73—76, 1904 and 1905, especially No. 11., Vol. 73.

of the darkened leaf may be found to have gone up to the original level, to fall off quickly again on further starving.

It is of great additional interest to note that however much assimilatory sugar is thus given, the respiration is not brought above the original level, but is only enabled to persist the longer at that level. This we interpret as meaning that the respiration of a fully nourished leaf is limited by the amount or mass of the respiratory enzyme or "enzyme branches of the protoplasm" present in the cells, the sugar being in excess. Here we have a first clue to the nature of the biological regulation of a single function in the plant-cell: one can conceive that were it desirable, for purposes of growth, for example, to increase the energy-providing oxidation, then the mass of enzyme present would be added to. In other cases and for other reasons it might be required to reduce the amount of enzyme. The consideration of how new enzyme particles are formed is quite above the level of our present knowledge, but we have seen how they may be destroyed in discussing Albert's work on the ultimate hydrolysis by a proteolytic enzyme of the zymase of etherised yeast-cells.

That such changes go on in living cells has been admirably shown by Czapek<sup>1</sup> for one very interesting case. In the cells of the roots of *Vicia*, homogentisinic acid is continually being formed from tyrosin by the action of an enzyme, but the acid so formed does not accumulate, but is, in its turn, destroyed by an oxydase. The amount of homogentisinic acid present is thus the balance between two opposed reactions. It fortunately happens that the amount of this acid can be accurately determined by titration of the extract of the roots by means of silver nitrate.

Czapek found that the mere fact of placing a root horizontal instead of vertical brought about an increase in the amount of homogentisinic acid present. This he attributes to the formation of an "anti-enzyme" which stops the action of the oxydase, whose function it is to destroy the acid. This effect seems to be a fairly direct result of the geotropic stimulus resulting from the horizontal position, since it comes on before curvature, (being at its height in 30 minutes and then passing away), and it is produced even on the klinostat, where no actual curvature takes place because the stimuli are continually counteracting one another.

This is the first case of a direct demonstration that the rate of enzyme activity in the cell is in close correlation with external

<sup>1</sup> *Annals of Botany*, XIX., Jan., 1905.

stimuli, even with those like gravitation, that do not appear to affect the protoplasm through a chemical mechanism.

A regulating effect of mass of yet another order must now be mentioned. The rate of action of a hydrolytic enzyme might in theory be affected by the amount of water molecules available for uniting with the substance to be hydrolysed. As in practice such changes take place in aqueous solution only, there is an enormous excess of water-molecules always present, and the mass of the water never acts as a limiting factor and may be neglected.

With an oxidising enzyme, it is the union of some substance with hydrogen-dioxide (or with a similar "active" peroxide) and not with water, that is accelerated by the katalytic agent. This active peroxide will not necessarily be present in excess, and may be a limiting factor. Its varying amount will then determine the amount of oxidation that is being performed, and regulation may be obtained in this way. There seems to be no doubt that an active peroxide is present in the normal cell to a certain extent but we are unacquainted with the precise mechanism of its formation.

Chodat and Bach in their interesting and accurate study of oxidising enzymes previously referred to have shown how such effects of mass interact. They investigated the amount of pyrogallol that could be oxidised by hydrogen dioxide to form purpurogalline under the accelerating influence of an oxidising enzyme prepared from horse-radish. Varying amounts of (1) pyrogallol, (2) hydrogen dioxide and (3) the enzyme-extract were mixed together, and after fourteen hours the crystalline, insoluble purpurogalline was filtered off, washed, dried and weighed. A quite precise relation holds between the amount of it formed and the amount of that one of the three original substances which happens to be the limiting factor to the activity of the whole system.

The following Table is compiled from their figures, and shews how the amount of the product may be regulated by the amount of either of the reacting substances.

EXPERIMENT.	A.	B.	C.	D.	E.	F.	G.	H.	
Pyrogallol ...	1·0	1·0	1·0	1·0	1·0	1·0	1·0	2·0	gm.
H <sub>2</sub> O <sub>2</sub> ...	1·0	1·0	1·0	1·0	0·8	0·4	0·1	1·0	cc.
Enzyme ...	·01	·04	·08	·10	·10	·10	·10	·10	gm.
Purpurogalline	·02	·08	·16	·16	·16	·08	·02	·20	gm.

In A and B the enzyme is limiting; in C the maximum of purpurogalline obtainable from 1 gm. of pyrogallol is already reached and this limits C, D and E: H proves this by showing that with increase of pyrogallol more purpurogalline is obtained. In F and G the hydrogen dioxide is limiting.

It follows from this table that when 0.8cc. of hydrogen peroxide reacts with 1 gm. of pyrogallol in presence of .08 of enzyme extract, neither of the three is in excess, but all are just equivalent.

From the various investigations recounted in this article we may fairly well conclude that, though the process of enzyme formation is yet obscure, the quantitative activity of existing enzymes and metabolic changes in the living cell must be governed by simple physico-chemical principles.

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## SOME GENERAL ASPECTS OF THE ALGÆ.

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Morphologie und Biologie der Algen von Dr. Friedrich Oltmanns. Zweiter Band, Allgemeiner Teil. Pp. vi. and 443, 3 Plates and 150 figures in the text. Jena, Gustav Fischer, 1905.

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WITH the publication of the second (general) part,<sup>1</sup> Professor Oltmanns' great Hand-book of the Algæ is completed. The system pursued in the present volume is to take various topics separately and to treat them generally and comparatively with regard to the Algæ as a whole. The volume is divided into eleven chapters and each of these is devoted to one of these topics, which are as follows: System of the Algæ, Development of Reproductive Organs, the Algal Cell, Nutrition, Conditions of Life, Periods of Vegetation, Phenomena of Irritability, Polymorphism, Alternation of Generations, Adaptations, Methods of Investigation. It will be seen that this scheme includes a great many, though by no means all, of the general points of view from which the Algæ can be considered. Certain topics which might with advantage have been included at once suggest themselves, for instance the Phylogenetic Relation of the Algæ to the rest of the Vegetable, and to the Animal Kingdom, the Place of the Algæ in the Economy of Nature, the Tissue Systems of the Algæ considered both morphologically and physiologically. But it may be admitted that it is unreasonable

<sup>1</sup> The first (special) part of this work was reviewed in the NEW PHYTOLOGIST, Vol. IV., p. 85.

to expect any single author to deal exhaustively with the subject in this way.

In dealing with the system of the Algæ, a short historical summary is given, but the author makes no attempt to undertake the laborious and rather useless task of assigning to each writer the suggestions original to him which have become incorporated in the modern system.

Professor Oltmanns himself, as was clear from his first volume, adheres to the main fundamental principles of the Swedish algologists, who hold that the structure of the algal cell, and especially of the different types of zoospore, which are to be regarded as survivals of the different primitive flagellate forms from which the various groups have been derived, is the basis on which the primary division of algal forms should rest. The roots of the various algal series are thus found among Protista, and it is impossible to lay down precise limits as to where the Flagellata end and the Algæ proper begin. On each of these phylogenetic series sexuality (in the sense of gamogenesis) has been acquired, sometimes more than once on different branches of the individual series; and the sexual process nearly always shews a progress from isogamy to oogamy. Although our author anticipates that these views will awaken doubt and even contradiction, for our own part we have not the least misgiving in considering them at the present time perfectly well established principles upon which all further advance must be based. At the same time Professor Oltmanns has a wise word of warning to the effect that *all* the characters of the cell must be taken into account in making the primary divisions; and although colour and cilia are apparently the most important from a taxonomic standpoint, there is, of course, no *a priori* barrier to the evolution of a multi-ciliate from a bi-ciliate zoospore, nor of a red or brown from a green cell. Something of this sort has apparently happened in the Peridineæ.

Concerning the actual system adopted by Professor Oltmanns it is not necessary to say much here, since the principal points in which we differ from him have been fully discussed in our review of the first part of the present work.<sup>1</sup> We may, however, again refer to the undesirability of grouping the Diatoms and the Conjugatæ together under the title of Akontæ (a word which was introduced for the Conjugatæ alone) whatever views may be held as to a possible common origin. Professor Oltmanns himself admits, in a footnote,

<sup>1</sup> NEW PHYTOLOGIST, loc. cit.

that Karsten's recent discovery of numerous gametes in the Plankton diatom *Corethron*, makes many of his (Oltmanns') conclusions "again doubtful," and we cannot but think that the origin of both the Diatoms and Conjugates is still wrapped in profound mystery.

With the remarks on the Volvocales and Protococcales we are in close agreement. The treatment of Ulotrichales and Chætophoraceæ reveals nothing very new; the possibility of deriving the peculiar zoospore of *Ædogonium* from the bi-flagellate type is discussed and the fact that the two flagella of such a zoospore as that of *Cladophora* are not really terminal, but arise on each side of a terminal papilla, is brought in evidence. The Chætophoraceæ and allied families are derived, as usual, from the Ulotrichaceous type, but their treatment here is decidedly meagre.

The Siphonocladiales are derived from uninucleate cell-types such as the Ulotrichaceæ by division of the nucleus, rather than by the septation of the Siphoneous plant, while the Siphonææ proper, it is suggested may have arisen from the Siphonocladiales by suppression of thesepta, through the Codiaceæ. The Siphonocladiales are also thought to have given rise to the Verticillatæ, through *Dasycladus*, and to the Caulerpacææ, through *C. fastigiata*, so that the septate cœnocytic group would thus become the common ancestors of the whole of the Siphonoideæ.

This possibility cannot be altogether neglected, but the line of evolution indicated involves a wholesale reduction of structure which necessitates rather an unwieldy hypothesis, and one scarcely to be adopted without more cogent arguments than are adduced. We prefer to adhere for the present to the simpler hypothesis of the evolution of the Siphonææ from the Protococcales through a form like *Protosiphon*, since the "siphoneous tendency" is clearly indicated within the latter group.

Professor Oltmanns is evidently not altogether satisfied with the position of *Vaucheria* as belonging to the Siphonææ, though he suggests a comparison with *Codium*; neither is he quite willing to accept Bohlin's view. The position of *Vaucheria* must remain still very doubtful.

The old-fashioned view of the connexion of the Rhodophyceæ (from which the Bangiales are altogether excluded, as more naturally placed with Prasiolaceæ) with Colcochæte does not find much favour in Professor Oltmanns' eyes, and in this we certainly sympathise. But he inclines to the opinion, especially on the ground of the striking parallelism of their "sporophytes," that the Florideæ



have some real genetic relationship with the Ascomycetes, or with the Laboulbeniaceæ. This is the kind of suggestion of affinity, however, of which we have an instinctive distrust in the absence of the strongest evidence in the way of intermediate forms, and we hold it far more likely that the whole phenomenon is one of those elaborate pieces of parallelism in which the organic world is so rich. In any case the Florideæ-Ascomycete hypothesis does not contribute towards the solution of the problem of the origin of the Red Seaweeds. The true affinities of the Florideæ must, we think, still remain a profound mystery.

Professor Oltmanns leans strongly to the view of a separate flagellate origin for the Brown Seaweeds, on the ground of the specially characterised swarmer. Among the simple brown forms, however, which Scherffel put together to form a series, leading from the Flagellata to the Phæophyceæ, only *Phæocystis* has a swarmer of true Phæophycean type, so that while we consider the separate origin of the Phæophyceæ an extremely plausible hypothesis, we must admit, as Professor Oltmanns says, that we do not know from what existing Flagellates they could have been derived.

The treatment of the internal phylogeny of the Brown Seaweeds is, we think, one of the most satisfactory parts of this section of the work. The degree of sexuality will clearly not do as a primary principle of division; we must adhere to the structure of the thallus for this purpose. The Ectocarpaceæ are taken in a much wider sense than usual, and from this great primitive group, the Laminariaceæ are derived through *Chorda*, the Asperococcaceæ through *Myriotrichum*, the Mesogloeo-Chordarian series, as Professor Oltmanns calls it, and the Cutleriaceæ on another side, and finally the Sphacelariaceæ and Tilopteridaceæ along parallel lines. The disc-forming types are in all cases considered as reduced forms. The details of this, to our mind very luminous, arrangement, are to be found in the Special Part (pp. 348 et seq.) of the work. The Dictyotaceæ, on the ground of the general characters of the cell, and on the basis of Lloyd Williams' discovery of motile antherozoids, are very rightly united with Fucaceæ as Cyclosporeæ, the existence of the so-called tetraspores being quite insufficient to link them with the Florideæ. While it is not difficult to homologise the sexual organs of Cyclosporeæ with the plurilocular sporangia of Phæosporeæ, it is not easy to say from which group of the latter the former have been derived.

In the second chapter of the work a general account is given of

the processes of development and escape of zoospores and gametes. The zoospores produced by an algal cell are regarded as being modelled from the middle region of the layer of protoplasm surrounding the central vacuole, each round a definitively formed nucleus. In this way the hyaloplasm of vacuole wall and ectoplasm come to be left over, together often with a certain quantity of interstitial protoplasm. Ectoplasm and vacuole wall are not regarded by the author as having an autonomous existence as special organs of the cell.

In his general remarks on the developmental processes of the female gametes, Professor Oltmanns concludes that none of the processes of maturation, not even the striking phenomena exhibited in the Fucaceæ, can be directly compared with the formation of polar bodies by the animal egg, since polar body formation is so constant that it must presumably have a universal significance, while the phenomenon of "cast-out" nuclei in Fucaceæ is entirely dependent on the number of mature eggs to be formed in the oogonium. Professor Oltmanns compares this last phenomenon rather with the production of nutritive or follicle cells from the sister cells of eggs in Daphnidæ and Insects. He does not, as we understand him, deny that in all such instances (including polar body formation) the cells which do not become eggs are to be regarded as reduced members of a brood of gametes—as Hartog long ago pointed out—of which the functional egg alone becomes mature and develops at the expense of its sisters, but he thinks that polar body formation is a specialised case of this, connected with the reduction division, and only to be indirectly compared with the phenomena found among the algæ. The somewhat mysterious behaviour of the nuclei discovered by Klebahn in certain Diatoms our author considers as the remnant of an ancestral formation of a brood of gametes such as Karsten finds in *Corethron*, while the two nuclei in each of the two embryos formed from the zygotes of *Cosmarium* and *Closterium* are similarly supposed to be reminiscent of ancestors, which, like the Mesotæniaceæ, normally produced four embryos from the zygote. Professor Oltmanns' conclusions appear to take us as far as we can safely travel in the light of the facts at present known. Whether any or all of the nuclear phenomena in question can also be related to the process of chromosome reduction, which must take place at one stage or other of the life cycle in all sexual forms, the future alone can show.

There is a good general account of the conditions under which

gametes are liberated and of the phenomena of fertilisation,<sup>1</sup> but the discussion of the homologies of the reproductive organs is not entirely satisfactory. Professor Oltmanns, of course, homologises all gametes and (most) zoospores. That, of course, is common ground, but we think his exposition would have gained in simplicity and clearness if he had laid stress on the swarmer as the direct representative of the vegetative individual of the primitive motile forms derived from the Flagellates. Whether it is or is not capable of conjugation in any particular case is of very little consequence from the broad phylogenetic standpoint. The view put forward by Professor Oltmanns that all zoospores are not necessarily homologous, some having probably developed independently, is, in our opinion, unlikely in the highest degree. The hypothesis of the development *de novo* of so specific a structure as the motile flagellated cell from a motionless algal cell, when there is the best general ground for the belief that the motionless cells in question had flagellated ancestors, seems to us to amount to the artificial manufacture of phylogenetic difficulties. The synzoospore of *Vaucheria* is no doubt an organ of a peculiar composite nature (like the syngametes of certain Fungi), but it is no more an organ *sui generis* in the strict sense than (say) a Composite inflorescence is. Its existence is, in our view, rather an argument against supposing *Vaucheria* to represent an offshoot of the Siphonæ.

A considerable section of the work is devoted to the algal cell; cell-wall, protoplasm, nuclei, centrosomes, karyoids, chromatophores and vacuoles being treated separately. Of these the cell-wall, and especially the chromatophores, on account of their great variety of form and structure, occupy the most space. The treatment of the nucleus strikes us as too slight. Fragmentary as our information on the cell-nuclei of the Algæ still is, some more serious attempt should have been made to sum up the conclusions that may be drawn in regard to its structure, function and evolution.

The impression left by Professor Oltmanns' accounts of the cell-wall and chromatophores is of the extraordinary diversity of these structures among the Algæ, due to the number of different experiments Nature has tried in these fields and to the variety of conditions, mechanical and illuminative, under which the Algæ exist. The chromatophores, in respect of their relative constancy and

<sup>1</sup> We can confirm, from personal observation, Chmielevsky's account of the degeneration of the chromatophore belonging to the male gamete in the zygote of a certain species of *Spirogyra*, an account as to which Professor Oltmanns seems to entertain some doubt.

variability in the different species and genera, are happily compared with the leaves of the higher plants. The general phylogenetic considerations that are given, however, are not so fortunate, and Schimper's view is, we think, rather unfairly treated. The author seems to fall into the too common mistake of supposing that the conditions obtaining in growing points can give information as to primitive ancestral stages. Though Schimper's theory cannot be expected to express satisfactorily the modern standpoint involving the polyphyletic flagellate origin of many at least of the algæ, it probably contains a large part of the truth, and an attempt should be made to re-state it in the light of our knowledge of the primitive chromatophores of the Volvocaceæ on the one hand, and the lower Heterokontæ on the other.

In the section on Pyrenoids there is no reference to the work of Timberlake (Annals of Botany, 1901) who showed, for *Hydrodictyon*, that the apparently fundamental difference between "pyrenoid-starch" and "stroma-starch" hypothesized by Klebs has no real existence, the so-called stroma-starch being merely grains of pyrenoid-starch pushed out into the substance of the chromatophore. Whether this applies also to the other pyrenoid-bearing forms in which stroma-starch can be demonstrated, has not, so far as we are aware, been shewn, but Timberlake's careful method of investigation certainly ought to be applied to such forms.

In the chapter on Nutrition, a condensed account is given of the available information on inorganic food-stuffs, gaseous exchange, respiration,  $\text{CO}_2$ -assimilation, nitrogenous and non-nitrogenous reserves, and finally of nutrition by organic substances. Here, as elsewhere, the references to the work of the various investigators are extremely full and will be most useful alike to the advanced student and to the specialist.<sup>1</sup> One of the interesting points that is brought out is the much greater extent to which algæ can avail themselves of ammonium compounds and more complicated organic nitrogenous substances (even of peptone) than is possible to the higher green plants, which mostly depend on nitrates. No doubt this is to some extent correlated with the large amount of organic substances, produced by the decay of organisms, present in the freshwater inhabited by many green algæ; but it may be also attributed to inheritance from the holozoic and saprophytic flagellates from which the green algæ at least are descended.

The fifth chapter deals with the Conditions of Life among

<sup>1</sup> There are no less than 162 references to literature attached to this chapter of the work alone.

Algæ, and contains excellent discussions of the factors which affect the distribution of the different groups and species. Though the ecology of algæ is yet in its infancy, there are a good many observations on record, and Professor Oltmanns makes the most of these.

It is pointed out that it is impossible for algæ to gain a hold on a sandy or muddy sea-bottom liable to constant shifting by the tide, though certain forms can do so where the substratum is comparatively at rest. Single rocks or any resistant substratum such as a pier or pile in such a shifting area always furnishes a place of attachment and gives rise to an algal oasis in the desert.

A good account is given of the zonation of algæ on a coast and it is shewn to depend partly on mechanical adaptation and partly on light, but also on the different facilities for the supply of food, and particularly oxygen, available in relation to spray, waves, etc. Another interesting section deals with the composition of the medium, particularly in relation to salt-content. The diminution of salt in the Eastern Baltic (from the 3·5%, which is the normal oceanic salinity, to ·74% and even to ·15%) is shewn to cause a considerable decrease in the number of species of marine algæ, many of which cannot adapt themselves to such conditions. The extraordinary vegetation of Warnemünde is described. Here *Phragmites communis* and *Fucus vesiculosus* flourish side by side. *Potamogeton pectinatus* bears *Ectocarpus*, *Polysiphonia violacea* grows on *Myriophyllum*, while *Spirogyra* and *Chara* occur between. This is in a salt-concentration of ·5%. Though the brown and red genera mentioned can tolerate such a small amount of salt, most of their congeners cannot. *Ulva*, *Enteromorpha* and *Cladophora* on the other hand, are the most indifferent to such changes, as is well known. Not only can they flourish in almost fresh water, but they can also tolerate high salt concentrations up to 10% and 13%, though they can only flourish in salt solutions of somewhat less strength. They may be called *euryhaline* as opposed to *stenohaline* species such as most of the Floridæ and Phæophyceæ. The euryhaline habit depends directly upon the power of these algæ to take in salts from outside and thus temporarily raise the osmotic strength of the cell-sap. Again some forms can bring about these osmotic alterations quite rapidly, while others cannot. All these factors clearly control the possible habitats of the various forms in relation to salt-content of the medium. The possibility of permanent migration from salt to fresh water and *vice versa* must also depend upon the acquirement of similar powers. The salt-relation has considerable taxonomic importance. Most of the unicellular green forms are exclusively fresh-

water, while many of the filamentous forms (though apparently none of the isogamous ones) live both in the sea and also in freshwater. Practically all the Siphonæ are marine, and nearly all the Floridæ and Phæophyceæ (mostly stenohaline forms). The exceptions among these latter groups may have wandered up through the brackish waters of river mouths to the mountain streams they mostly inhabit, or they may be the more resistant remnants of a marine flora in areas formerly covered by the sea.

The remaining sections of this chapter deal with Temperature and Light. The latter is, of course, the more important as an ecological factor, though the relations of the different algæ to it are by no means completely understood. While the facts of zonal distribution of the red, brown, and green forms support in a general way the well-known Oerstedt-Engelmann theory, yet the correspondence is by no means so complete as to satisfy us completely. Oltmanns' own observations, and Berthold's also, seem to shew that in many cases the Floridæ behave rather as shade plants than as green-light plants, *i.e.*, they live in weak white light rather than in spectrally selected light. In spite of Gaidukov's striking observations<sup>1</sup> on complementary chromatic adaptation in *Oscillaria*, the variations in the pigment of various Floridæ are not easily explained on his principles. Much more experiment, as well as observation in "freie Natur," is required before these problems can reach anything like a definitive solution. Meanwhile it is, we think, impossible to doubt that the "complementary" principle must play an important, perhaps the leading, part in colour determination.

Professor Oltmanns has some interesting remarks on methods of protection against over-illumination. It appears that *Fucus*, *Codium* and the Rhodomeleæ tend to cover themselves with hairs when exposed to strong light. These colourless hairs, so widely spread among marine algæ, have often been considered as respiratory. They may also, Professor Oltmanns thinks, be of use because they increase the food-absorbing surface. The iridescent colours of many red seaweeds are due to reflecting masses or layers of substance immediately below the external cell wall, and these probably serve to decrease the amount of light reaching the chromatophores.

In the chapter on Periods of Vegetation it is shewn that in temperate regions the great vegetative period is the spring, and this applies in a general way to marine and freshwater forms, to Benthos and Plankton alike. The summer flora of the more northern seas may be regarded as a continuation of the spring vegetation, owing

<sup>1</sup> See "Chromatic Adaptation," *NEW PHYTOLOGIST*, Vol. III., p. 237.

to the later beginning of the vegetative period. In the Mediterranean the summer vegetation is very scanty. Another vegetative maximum, especially in Plankton, is reached in the autumn. This double curve is attributed, on good grounds, to seasonal light variations rather than to those of temperature. The light is supposed to be too weak in winter and too strong in summer for active assimilation and therefore growth. The heat factor cannot, however, be wholly excluded. The striking fact is brought out that the typical green freshwater algæ æstivate and hibernate in the form of resting cells—hypnozygotes or hypnakinetes—while the typical red and brown marine forms pass their resting periods in the vegetative condition, usually dying down more or less completely—except in the case of the “evergreen” Fucaceæ and Laminariaceæ—and shooting out again at the beginning of the next vegetative period. This phenomenon is correlated with the more equable temperature of the sea, and it is pointed out that the freshwater Florideæ, which inhabit mountain streams, are also exposed to less variable temperature conditions than the inhabitants of ponds and ditches.

The chapter on the Phenomena of Irritability is divided into two parts, the first dealing with Directive, the second with Formative Stimuli. Under the heading of Phototaxy and Phototropism, a neat arrangement is figured for shewing that at a certain light intensity—the “optimum”—motile cells sensitive to light move neither towards nor away from the region of greater intensity, but perform a slow upward movement which is probably geotactic. As might be expected, the phenomena of response to directive stimuli are fundamentally the same as those met with in the higher plants, though they are often much less markedly developed.

Under “Formative Stimuli” a great deal of interesting information is brought together, particularly in relation to “Wound-Stimuli,” though but little synthesis is possible. Most of the section on the effect of conditions on the formation of reproductive cells is taken from Klebs’ well-known work. Here also generalisation is scarcely attempted, though Klebs’ distinction between “antecedent conditions” and “releasing stimuli” is maintained. The difference in the reaction of various algæ to the same substances is certainly often very puzzling, though, we think, an attempt to find a clue through at least a considerable part of the labyrinth might have met with success. The *Palmella* forms of various algæ are considered as relatively “passive states” induced by conditions under which normal growth or reproduction are no longer possible.

The next two chapters are very short, and are devoted to

“Polymorphism” and “Alternation of Generations” respectively. On Polymorphism Professor Oltmanns is very decisive, taking up Klebs’ position on the facts, and preferring, as we think rightly, to drop the much abused word altogether. “Für mich,” he says, “hat das wort aber einen so üblen Beigeschmack, dass ich es am liebsten ganz streichen möchte, es hat zuviel Unheil gestiftet.” He shews, in fact, that so far as the phenomena are real at all they are better placed under other concepts.

In his treatment of Alternation of Generations Professor Oltmanns adheres to the view of the “antithetic” origin of the Archegoniate sporophyte and regards the zoospores produced as an immediate result of the germination of the zygote in *Hydrodictyon*, *Sphaeroplea*, *Coleochaete*, *Ædogonium*, etc., as rudimentary developments of the same kind, these zoospores (carpospores) being sharply separated from the zoospores produced by a potential gametophyte. With Klebs he denies the existence of a true alternation in *Vaucheria*, but in a case like *Dictyota*, he concedes the possibility of a “homologous” origin of the two generations.

The chapter on “Adaptations” occupies a quarter of the whole book. It is pointed out that the external conformations of the Algæ can be grouped in categories to each of which belong species of very various affinity. In some of these cases an attempt is made to find the adaptive significance of the vegetative form in question, while in others the author confesses his inability to do so. The forms distinguished are Shrub and Tree-forms, “Mucilage-bush”-forms, Whip-like forms, Net-algæ, Leaf forms, Bladder forms. Dorsiventral Algæ, Bolster-, Disc- and Crust-forms. *Bryopsis* is a good example of the common Bush or Tree form in which the whole plant-body may be compared with a leafless tree, or better, with a plant like *Asparagus*; light has relatively free access to all assimilating parts of the plant. This is a useful arrangement in the case of plants like algæ, the whole of whose bodies are, on account of the absorption of light by the medium, exposed to shade conditions. Various methods by which the different branches are kept apart are described. The “mucilage-bush forms,” such as *Chlorodendron*, *Mischococcus*, etc., are regarded as a special case in which the mucilage serves to keep the branches—here composed of separate cells—apart and relatively rigid. The Whip-forms (*Ulothrix*, *Himantalia*, etc.) are regarded as adaptations to water movement. Net-algæ (*Hydrodictyon*, etc.) on the contrary, are considered as adapted to the maximum bathing by the medium in still water, though in some cases (*Struvea*, etc.) other factors are probably



responsible. The Leaf-form is recognised, here as elsewhere in the plant-kingdom, as a primary adaptation to light, and its modifications are discussed.

It is, of course, sufficiently obvious that the fact of these various vegetation-forms being well fitted to live under the various conditions in which they occur is no explanation of the *origin* of the forms in question, since algæ of various forms live side by side, and we are often quite at a loss to understand the origin of their differences *inter se*.

The various types of Epiphytes, Endophytes and Parasites are fully described and illustrated, and the transitions between them indicated.

A very useful section is devoted to Plankton. The literature of this subject has increased enormously in the past decade; it is very widely scattered and much of it is rather inaccessible. Professor Oltmanns brings together the main facts and principles in his short but judicious account.

The adaptations of algæ which live partly or wholly out of water also forms the subject of a short section, and the different forms are distinguished. While some, mostly unicellular forms (*Pleurococcus*, etc.), simply lie or are fixed in situations where they are liable to drying, a few others—*Protosiphon*, *Botrydium*, *Ædo-cladium*, species of *Vaucheria* and *Stigeoclonium*, are strictly terrestrial, and have an absorbing root system like the higher plants. The former not only resist drying up with great success, but in some cases it has been shewn that long drying is necessary to their resting cells to enable them to germinate.

In the section on Symbiosis, a short account of Lichens is given, and then the association of unicellular algæ with various animals is described. In regard to the green cells of *Convoluta Roscoffensis* attention should be called to the work of Keeble and Gamble,<sup>1</sup> who have made a very full study of this particular case of symbiosis, correcting many of the older statements. These authors have quite recently<sup>2</sup> shewn that the alga is a quadri-flagellate *Chlamydomonas* which enters the young animals from the egg capsules, on which a rich flora lives. It is interesting to notice that in one of Haberlandt's figures reproduced by Professor Oltmanns, the whole structure of the "green cell" shewn corresponds exactly with the *Chlamydomonas*-type.

Finally an account is given of the symbiosis of various algæ with Sponges.

<sup>1</sup> Quart. Journ. Micr. Sci., 1903.

<sup>2</sup> Proc. Roy. Soc., B. 77, 1905.

The last chapter of the work is devoted to a consideration of the technique of phycological investigation. Research-stations, methods of capture and transport are dealt with, and there is a very useful section on the culture of algæ, in which methods the author has himself used with success are described.

In concluding this somewhat lengthy review, in which an attempt has been made to give the reader some idea of the contents of Professor Oltmanns' comprehensive work, we may reiterate the opinion that those generalisations, occurring particularly in the earlier part of the present volume, which refer to particular groups, would have been better included in the Special Part. This would have rendered the treatment of the different groups more complete and interesting, and would have allowed of more general summaries in the present part. The other general remark which we have to make is to express regret that Professor Oltmanns has not attempted a synthetic treatment, and particularly an evolutionary treatment, of his subject matter in a greater number of cases. We feel sure this could be done with success in many instances, and such treatment is of the highest value when undertaken by such a master of his subject as the author of this work. The amount of information contained in its 1100 odd pages, and the skill displayed in its arrangement and detailed discussion is most striking, and we must warmly congratulate Professor Oltmanns on having brought to a conclusion this magnificent compendium of existing knowledge of one of the most fascinating and important groups of the plant kingdom.

A.G.T.

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#### A VOICE FROM THE PAST.

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THE morphologist of to-day who concerns himself with the relations of the great groups of plants is probably grateful to Hofmeister and other contemporary workers who elucidated the ground plan of their life histories. But if he penetrates to an earlier date and dips into the pre-Hofmeisterian literature he seems to move in a strangely unfamiliar world, in which the ordinary landmarks of the phylogenetic morphologist are hardly discernible. For the mystery of the double generation, which involves all the classes of plants from the Liverworts onwards, was still unprobed, and the whole series was regarded from the stand-point of the flowering plant—a thing of one generation that bore sexual organs.

The gametophyte of the fern, or prothallus, was the homologue of a cotyledon, and so it remained till it occurred to Suminsky (1845) that this was a special stage set aside for the production of the sexual organs.

But notwithstanding this serious limitation, at least one Botanist proved capable of a broad philosophic outlook on the

relations of the Cryptogams to the Phanerogams. This was the case with Carl Adolf Agardh, Professor of Botany in the University of Lund till 1835, and afterwards Bishop of Wermland and Dalsland. It is his son, J. G. Agardh, the well-known Swedish Algologist, who died only a few years ago at an advanced age, whose name will be familiar with the present generation of Botanists.

The views of the elder Agardh may be gleaned from a perusal of his "*Lehrbuch der Botanik*," a book in two volumes, which is accessible in a German translation that appeared in 1831—1832. The preparation of this translation would seem to indicate the existence of a contemporary interest in his writings, though the ordinary sources of information upon which reliance is generally placed pass them over in silence.<sup>1</sup>

This omission of the historian we now attempt to repair in slight degree; for the views of our author have a considerable interest at the present moment, and merit rescue from oblivion, though this be but transient.

We begin our task of piety by a quotation. The following passage gives us an unusually clear picture of the position reached by Agardh; how he reached it we shall see by and by.

"In view of their similarity in habit alone no one would be tempted to assert a natural or close affinity of *Equisetum* with *Casuarina* and the Conifers. For habit alone cannot be accepted as a sufficient criterion of close relationship so long as a supposed difference in reproductive methods forbids a close comparison. But on my theory (which is explained in the sequel) the case is entirely altered and these groups actually invite comparison. *Equisetum* seems to me to be related to the Conifers much as is *Osmunda* to the Cycads, so that here we have a transition from Cryptogams to Phanerogams which removes all abrupt barriers."

Our author then compares the male flowers of *Cupressus* with the strobili of *Equisetum* and points out that the agreement is much closer than with the male flowers of many other Phanerogams. He then continues:—"The existence of a lacuna in the recent vegetation between *Equisetum* and the Coniferae strengthens rather than weakens my position, for it is just to this part of the system that so many of the forms belong that have become extinct during the revolutions of the world. The Calamites, Asterophyllites, *Volkmannias*, *Annularias* and giant *Equisetums* from Whitby; the wealth of fossil Conifers, Cycads and Ferns, the fruits of the Stonesfield Quarry, and so on—all these are relics of a vegetation that has gone long ago, leaving hardly any representatives behind. Such as they are, we find them often characterised by naked seeds and whorled cotyledons; they form a peculiar group, which in their day attained an expansion comparable to that of Dicotyledons and Monocotyledons in our own times. That a great gulf should exist between *Equisetum* and the Conifers is just what we should expect from these considerations."

That Agardh should have been able to reach this acceptable and even modern outlook so long ago as 1830 arose from his breaking with many of the false analogies that prevailed in his day of the relations between Cryptogams and Phanerogams. The

<sup>1</sup> They are not referred to in Sachs' well-known "*History of Botany*."

procrustean morphology in vogue at the time interpreted a fern-sporangium as a carpel or folded leaf, the annulus being regarded as the homologue of the midrib and the spores as the seeds.

Agardh breaks away from all this; he begins—"In passing from a condition of no vegetation to one of normal complex forms there must be intermediate types which connect the one condition with the other." He then proceeds to an analysis of the Cryptogamia generally, in which he draws attention to what we should call the homologies which he supposes to exist between the various types of sporangia of the former and the seeds and stamens of Flowering Plants.

Agardh sees in these sporangia the rudiments or incipient forms of the "normal" organ (*i.e.* seed or stamen). He expressly discriminates between the existence in Cryptogams of two sorts of organs, corresponding to stamens and seeds, and the question as to whether any sexual function is bound up in them. The latter he appears to have judged as improbable. No clear distinction is drawn between Homospory and Heterospory as we should now draw it, but the equivalents of seeds and stamens are located in different genera somewhat arbitrarily, as it must appear to the modern student.

In the case of the Leptosporangiate fern the sporangium is closely contrasted with a seed. The indusium is taken as corresponding with a carpophyll, whilst the placenta in each case is an equivalent organ; the stalk and annulus are compared with the funicle or raphe, whilst the contained spores are regarded as embryos, their number finding explanation in the recent discovery by Robert Brown of Polyembryony in the Gymnosperms. Agardh laments that "writers should have obscured the interpretation of these organs by naming the fern placenta a sporophor, the fruit a sorus, the seeds capsules, and the embryos seeds."

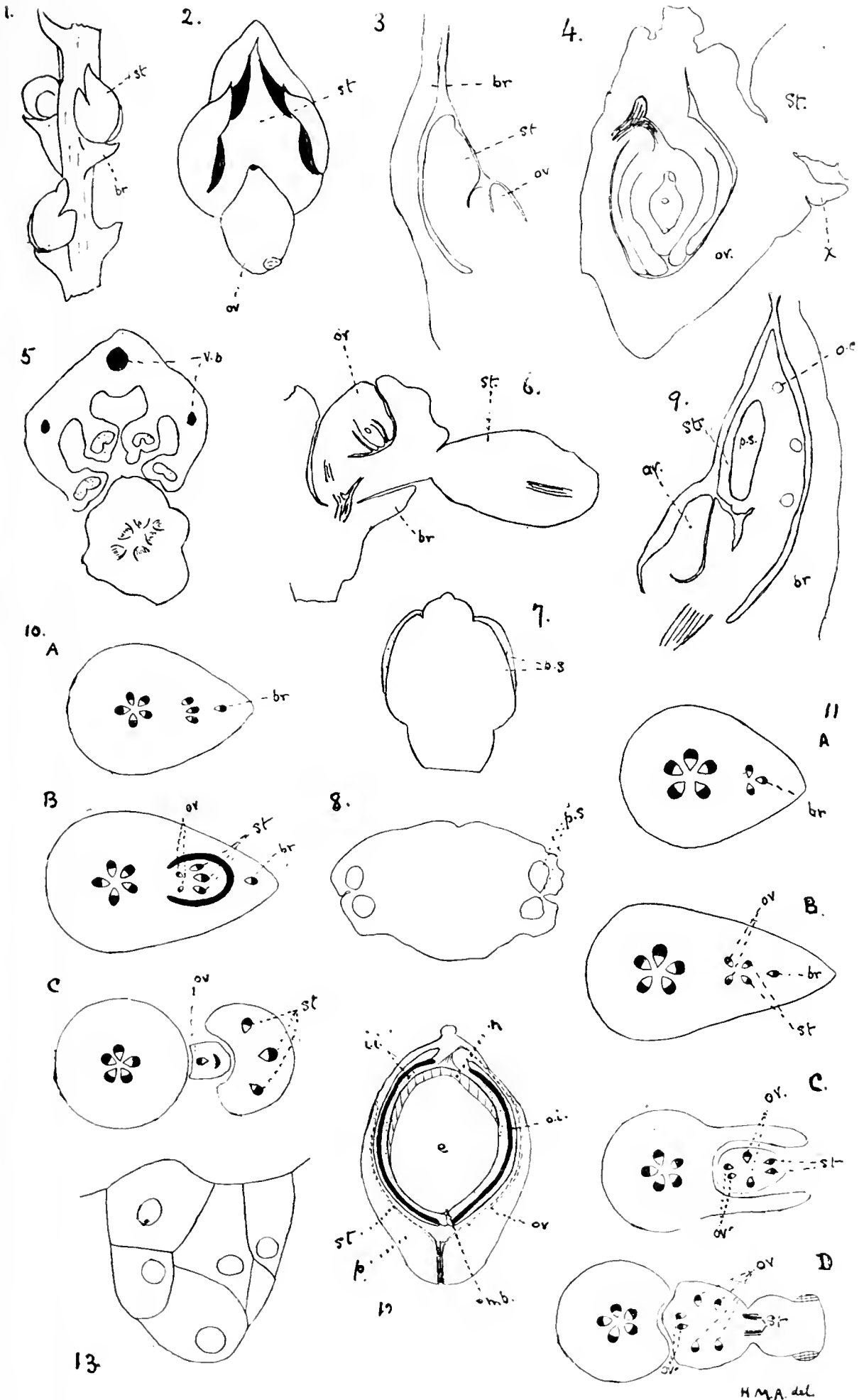
On the other hand the fertile spikes of *Ophioglossum* correspond with stamens, as also do the sporangia of *Lycopodium*, *Aneimia* and *Lygodium*.

Results obtained from contemporary attempts at spore-cultivation no doubt influenced Agardh in deciding the incipient sex of a given sporangium. Thus the difficulties still experienced in raising plants from the spores of *Lycopodium* would be a determining factor in favour of the staminal homology in the case of the sporangia; and the same would hold in other instances.

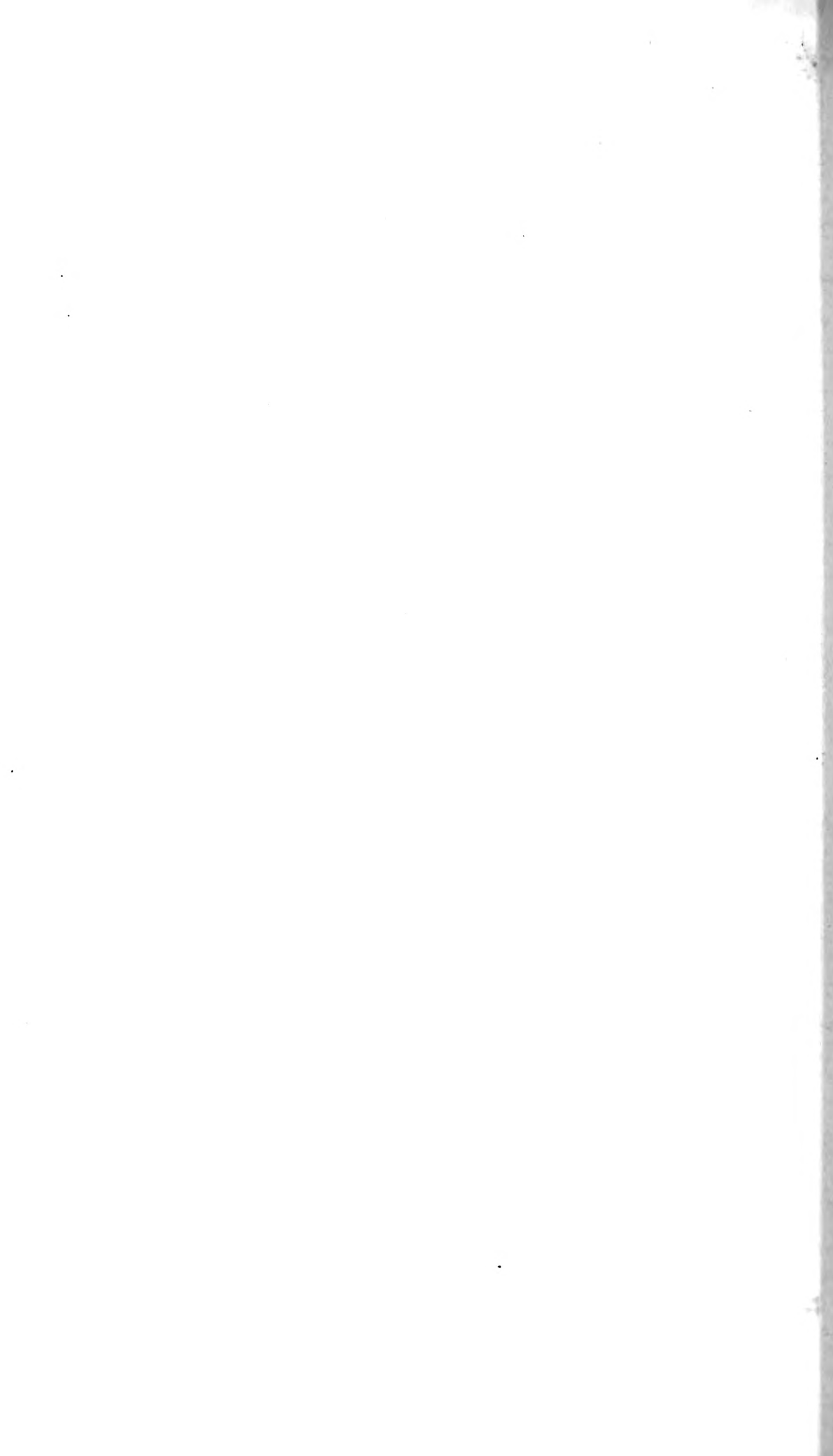
As a result of considerations of this sort three phylogenetic lines of descent emerge from the Cryptogams. First there is the Moss—Marsilea—Mniopsidaceae line<sup>1</sup>; secondly we have the Equisetum—Conifer—Casuarina line, and finally that of the Fern—Cycad. "That the seeds should be naked in Ferns is quite in keeping with the Cycadean relationship." Our author's scheme is fully abreast of views on the polyphyletic of the Phanerogams that became current many decades later.

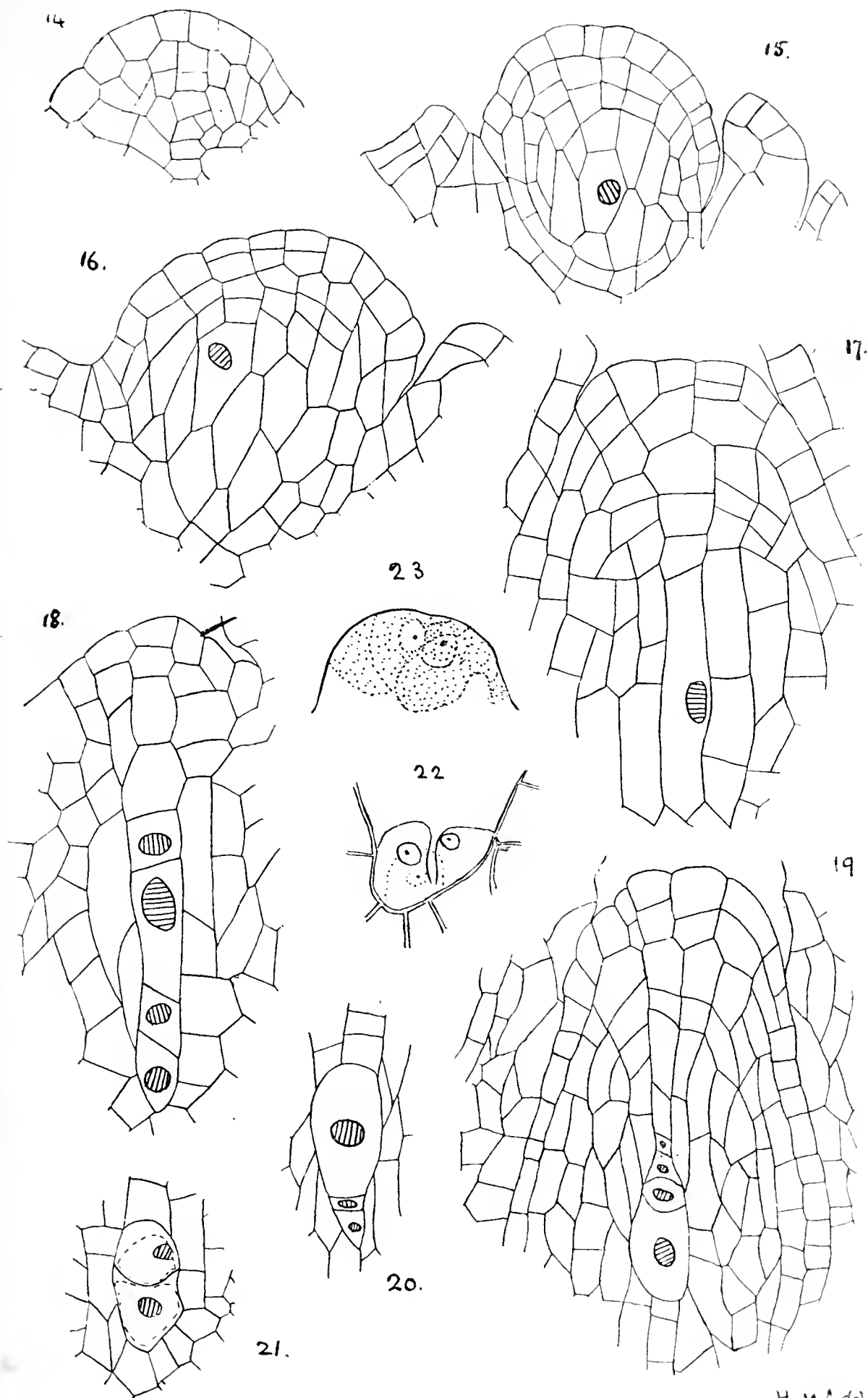
F.W.O.

<sup>1</sup> This is rather subtle, cf. *l.c.*, Erste Abt., p. 201.



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ON THE MORPHOLOGY OF CHLORANTHUS.

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[WITH PLATES III. AND IV.]

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OF late years some interest has been shown in the detailed morphology of the flower in the Piperales. Several genera of the Piperaceæ have been described, *Saururus* has been examined, but no corresponding study of representatives of either the Chloranthaceæ or Lacistemaceæ appears to have been made. In this paper are embodied the results of the investigation of the flowers of three species of *Chloranthus*. The material of *Chloranthus chinensis* was obtained from the Hakgala Botanic Gardens in Ceylon, and that of *C. officinalis* from Hakgala and from forests at Singapore. For some specimens of *C. brachystachys* from the Royal Botanic Gardens, Edinburgh, I am indebted to Professor Balfour. The preservation of the material collected in the tropics sufficed for the study of the morphology of the flower and the general structure of the ovule. Although the examination of better fixed material no doubt would show further points of interest, it seems justifiable in the present state of our knowledge of the Chloranthaceæ to record the results obtained.

In all these species of *Chloranthus*, the inflorescence is a spike with small, sessile flowers borne in the axil of a single tiny bract (Pl. III., Fig. 1). Each flower in *C. chinensis* and *C. officinalis* is composed of a staminal scale of three lobes inserted on an ovary which is one-celled and has a single pendulous orthotropous ovule (Fig. 2). The middle lobe of the staminal scale overtops the two lateral ones. The pollen sacs, which are eight in number and grouped in pairs (each pair resembling an anther lobe), are distributed so that four of them belong to the middle lobe and two to each of the two lateral lobes (Fig. 5). In *C. officinalis* the ovary is more bulky. The other species which was examined, *C. brachystachys*, shows a

thick, club-shaped staminal scale inserted on a massive ovary and almost at right angles to it (Fig. 6). This scale bears a pair of pollen sacs on either side (Fig. 8), and has usually been described as a single stamen. The ovary is large compared even with that of *C. officinalis*. In all species the stigma is tufted, and in mature specimens is shrivelled and withered.

The vascular supply to the flower in *C. chinensis* consists of a small bundle for the bract, and one large and two small vascular strands which pass from the axis into the flower (Fig. 10). The large bundle, which lies between the other two, traverses the median lobe of the staminal scale. The two small bundles, which enter the two lateral lobes, give off each a branch. These two branches soon fuse to form the single strand which supplies the ovary and traverses it up to the base of the ovule. *C. officinalis* also has three bundles supplying the staminal scale. The ovary supply, however, is derived directly from the vascular strands of the axis along with the staminal strands, and in several cases it consisted of more than one bundle. Usually the extra bundles are very small and difficult to determine in the earlier stages, but they were shown clearly in some of the ripening fruits. *C. brachystachys*, on the other hand, in addition to the single strand passing into the bract, shows six bundles entering the flower (Fig. 11). Two of these pass into the staminal scale and are at first quite separate, but just at the narrow insertion of the scale on the ovary they come close together for a short space (Fig. 8) and then diverge again to remain distinct up to the tip of the scale. The remaining four bundles enter the bulky ovary and there increase to six, two of these supplying the ovule, while the others run in the wall of the ovary.

Payer<sup>1</sup> found in the early stages of the development of *C. inconspicuus* that the median lobe of the staminal scale appears first, and that this is soon followed by the two lateral ones. These lobes are distinct in origin, but they immediately join to form the three-lobed scale. After some time, the pistil arises as a half-moon shaped outgrowth, whose convex side is towards the bract. As growth proceeds, the pistil forms a continuous ring of tissue whose edge is more raised on the anterior side.

The development of the pollen sac and pollen presented no unusual features. There was the typical division of the pollen mother cells into four, and the rounding off of the pollen grains, this process keeping pace with the development of the ovule. The anther lobe opens by a longitudinal slit. Numerous oil cells are

<sup>1</sup> Payer. "Traité d'organogénie de la fleur," p. 422.

present in the staminal scales of all three species, and were also found in the ovary wall (Fig. 9).

The youngest spikes of the available material showed the flower with its ovary having as yet no indication of ovule apparent. Fig. 3 is a median longitudinal section of the flower of *C. chinensis* at this stage. The ovule is first seen as a slight bulge on the adaxial side of the ovary wall, which forms a hollow cylinder with a very narrow lumen (Fig. 9). The passage or canal of the style is lined by a definite layer of small cells. There is no indication of integuments, but a number of prominent hypodermal cells are seen to have divided by periclinal walls. These cells represent the archesporial tissue, and the first division in them separates the sporogenous from the tapetal cells (Pl. IV., Fig. 14).

Fig. 15 shows a somewhat older ovule. The outer and inner integuments have been developed and the nucellus has increased in size and become more distinct. From the inner segments of the archesporium a group of cells is developed, distinguished by the size of the cells, the size of their nuclei, and their reaction to stain, as definitely sporogenous in character. The limits of this group are shown in median longitudinal section by narrow elongated cells on either side of it. The outer segments, or primary tapetal cells, undergo one or more periclinal divisions and over the sporogenous tissue form a cap that can be seen even in quite early stages (Figs. 15, 19). Shortly after this, periclinal walls form in the epidermal cells at the apex of the nucellus (Fig. 16). The innermost cells of the central mass within the nucellus become larger in size than the others, and have large nuclei. As the nucellus grows more bulky, the cells of the whole sporogenous mass increase in size, and one of them becomes distinguishable as the mother cell of the embryo sac. This is usually the lowest cell of the central column of cells in the sporogenous mass (Fig. 15), but in other cases a sporogenous cell in a lateral position becomes the mother cell. The ovule continues to increase in size, the embryo-sac mother-cell becoming most conspicuous by reason of its size and very large nucleus (Fig. 17).

After the embryo-sac mother-cell has attained its full length, it undergoes division by approximately transverse walls and forms a row of four cells. Of these four cells, usually only one develops further and becomes the single embryo sac. Its position in the row is by no means constant (Figs. 18, 19, 20). There was no indication of more than one sporogenous cell undergoing "tetrad" division. Several cases have, however, been observed in which two young

embryo-sacs were present (Fig. 21). These had evidently arisen by the simultaneous development of two adjacent segments of the mother-cell. After this stage, the development of the embryo-sac proceeds in the usual manner. Three antipodal cells, each with definite wall and a deeply staining nucleus (Fig. 22), are formed at the narrow basal end of the embryo-sac, and an egg apparatus at the micropylar end, while the two polar nuclei lie side by side in the centre of the sac. The fixation of the egg apparatus was imperfect, but it was observed to consist of three large cells with no definite wall, and with densely granular nuclei (Fig. 23). The largest of these cells is presumably the ovum, while the synergidae are in close contact with it. A section through the ovary and base of the staminal scale of a flower ready for fertilisation shows the position of the mature embryo-sac (Fig. 4). The micropylar end of the ovule is now directed to the base of the ovary cavity. Fig. 4 also shows the position at the insertion of the staminal scale of the small outgrowth which is frequently regarded as a perianth. The vascular bundle supplying the chalaza is seen to continue in the ovary wall for a short distance above the insertion of the ovule.

None of the specimens examined showed any trace of pollination, nor of the subsequent stages up to the formation of the young fruit. Apparently, however, after fertilisation does occur, the staminal scale breaks off at the place of narrow insertion, for it is not found on even the youngest fruits. In the fruit, three layers are clearly marked off (Fig. 12). The outermost is a somewhat thick succulent coat formed from the carpellary wall. Within it, and derived from the outer integument, is a hard fibrous layer whose inner margin of elongated cells represents the inner epidermis of the integument. The third layer is the inner integument, which forms a layer of thin walled tissue. In the seed, the nucellus has practically disappeared. At the basal end it persists longest, but there is nothing to suggest that its function is that of a perisperm. Within the seed-coats the space is thus occupied by the large embryo-sac filled with endosperm. The embryo, which is embedded in the endosperm, is small and shows no differentiation of its parts (Fig. 13).

The morphology of the flower of *Chloranthus* now falls to be considered in the light of the foregoing investigation. Upon this subject various opinions, expressed for the most part in systematic works, have been held. The flower has been regarded as composed of a male and female flower united together and looking like a single flower.<sup>1</sup> Most authors, however, have considered the flower to be

<sup>1</sup> Hooker. *Flora of British India*, Vol. V., p. 100.

hermaphrodite,<sup>1</sup> and examination of these species lends support to this view.

The small scale at the base of the insertion of the staminal scale upon the ovary is usually described as a perianth.<sup>2</sup> Celakovsky<sup>3</sup> regarded it as "a reduced incomplete perigone," and he considered its presence supports the general view that the flower is reduced. In the structure of this minute scale nothing appears to justify giving it such importance. The scale is present in *C. chinensis* and *C. officinalis*, but there is no trace of vascular supply. When the configuration of the developing flower is considered, it seems more reasonable to regard it simply as an outgrowth standing in relation to the rapid widening out of the staminal scale above its narrow insertion. In *C. brachystachys*, where the mutual relations of the parts of the young flower are different, it is absent altogether.

The staminal scale of *C. chinensis* has been described above as bearing four anther lobes, each composed of two pollen sacs. Usually these have been regarded as corresponding to three stamens, of which the median stamen has two anther lobes, and the lateral ones are reduced. With this view the vascular supply is consistent, but from development no evidence could be obtained of the reduction of the lateral stamens. If the flower were regarded not as reduced, but as tending in the opposite direction, other interpretations would evidently be possible, but the facts of development afford no positive support for such a view. The staminal scale in *C. brachystachys* is usually described as a single stamen. The position of the two anther lobes is that of the typical Angiosperm, but the presence in the scale of two vascular bundles appears to point to a comparison with the whole staminal scale of the related species. It is possible that the two pairs of pollen sacs correspond to the lateral pairs on the staminal scale of *C. chinensis*, the median stamen having disappeared by reduction. If this be so, the resemblance the scale bears to a single stamen is only superficial.

The facts ascertained are all consistent with the accepted relationship of the order of the Chloranthaceæ in the Piperales, and this may be briefly examined without extending comparisons beyond the series. The relative positions of the staminal scale and the ovary is not widely different from what is found in species of *Piper* and *Peperomia*, but whether the two, or three, stamens in *Chloranthus* are to be regarded as remains of the staminal whorls

<sup>1</sup> Payer. Loc. cit.

<sup>2</sup> Eichler's figure in "Blüthendiagramme."

<sup>3</sup> Celakovsky. "Über den phylogenetischen Entwicklungsgang der Blüthe, II.," Reprint p. 47.

of an ancestry with more complete flowers can only be decided on wide comparative grounds. Compared with the ovule in the Piperaceæ and Saururaceæ, that of *Chloranthus* is more bulky. The sporogenous tissue in it consists of a number of cells, and the embryo-sac mother-cell is apparent only at a comparatively late stage. The embryo-sac mother-cell undergoes a division in whose course presumably reduction takes place.

These are all points of similarity to other Archichlamydeæ usually regarded as primitive. The ovule of *Saururus* is intermediate between *Chloranthus* and the Piperaceæ, since in it the mother-cell of the embryo-sac undergoes division, while the subsequent development of the seed resembles *Piper*. In *Chloranthus* the mature embryo-sac and the later stages of development present no peculiar features. This tends to support Johnson's conclusion that "the peculiarities of the embryo-sac of *Peperomia* have been secondarily acquired."<sup>1</sup> The most probable conclusion from the floral structure appears to be that the Chloranthaceæ is a group of the Piperales presenting in some points, and especially in the structure of the ovule, primitive characters in common with the majority of the Archichlamydeæ, while in other respects special modifications of the flower are shown.

<sup>1</sup> Johnson: Bot. Gaz., Vol. XXX., 1900, p. 9.

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## DESCRIPTION OF PLATES.

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### PLATE III.

- Fig. 1. Sketch of part of a spike of *C. chinensis* showing position of the flowers. *br.*, bract; *st.*, staminal scale.
- Fig. 2. Flower of *C. chinensis* seen from the adaxial side, showing the ovary, and the three-lobed staminal scale with its pollen sacs. *ov.*, ovary; *st.*, staminal scale.
- Fig. 3. Median longitudinal section of youngest flower of *C. chinensis*.  $\times 55$ . The ovule has not yet developed. *br.*, bract; *st.*, staminal scale; *ov.*, ovary.
- Fig. 4. Median longitudinal section of mature ovary of *C. chinensis*.  $\times 40$ . The position of the ovule is shown. The outer and inner integuments enclose the nucellus in which is the large embryo-sac ready for fertilisation. *st.*, staminal scale; *ov.*, ovary; *x.*, so-called perianth.
- Fig. 5. Transverse section of staminal scale of *C. chinensis*, showing the position of the vascular bundles and anther lobes.  $\times 15$ . *v.b.*, vascular bundle.
- Fig. 6. Median longitudinal section of young flower of *C. brachystachys*.  $\times 15$ . *st.*, staminal scale; *br.*, bract; *ov.*, ovary.
- Fig. 7. Sketch of staminal scale of *C. brachystachys* seen from below. *p.s.*, pollen sacs.

- Fig. 8. Transverse section of staminal scale of *C. brachystachys*.  $\times 27$ . *p.s.*, pollen sacs.
- Fig. 9. Median longitudinal section of young flower of *C. officinalis*.  $\times 55$ . The ovule is apparent and oil cells are present in the staminal scale. *br.*, bract; *st.*, staminal scale; *o.e.*, oil cells; *ov.*, ovary; *p.s.*, pollen sac.
- Fig. 10. Diagrams of successive transverse sections illustrating vascular supply of *C. chinensis*. A shows one bundle coming off to the bract and three bundles to supply the flower. B shows the bract bundle, the three strands for the staminal scale and the two small branches coming off for the ovary. C shows the three staminal bundles and the single strand for the ovary, resulting from the fusion of the two small bundles seen in B. *br.*, bract supply; *st.*, staminal scale supply; *ov.*, supply to ovary; *ov<sup>1</sup>.*, supply to ovule.
- Fig. 11. Diagrams of successive transverse sections illustrating the vascular supply to the flower in *C. brachystachys*. Lettering as in Fig. 10.
- Fig. 12. Diagram of fruit of *C. officinalis* in median longitudinal section. The embryo is embedded in a mass of endosperm which almost entirely occupies the place of the nucellus. *emb.*, embryo; *e.*, endosperm; *n.*, remains of nucellus; *p.*, pericarp; *i.i.*, inner integument; *o.i.*, outer integument; *st.*, vascular supply to staminal scale; *ov.*, vascular supply to ovule.
- Fig. 13. Median longitudinal section of young embryo of *C. officinalis*.  $\times 455$ .

#### PLATE IV.

All the figures are of *C. chinensis*. The embryo-sac mother-cell and the cells resulting from its division have their nuclei indicated.

- Fig. 14. Youngest ovule in longitudinal section showing first division in hypodermal cells.  $\times 455$ .
- Fig. 15. Longitudinal section of slightly older ovule. The integuments are present and one of the sporogenous cells was recognisable as the embryo-sac mother-cell.  $\times 455$ .
- Fig. 16. A slightly older ovule showing divisions in the epidermal cells of nucellus, a definite sporogenous mass and a laterally derived embryo-sac mother-cell.  $\times 455$ .
- Fig. 17. Longitudinal section of nucellus of more mature ovule.  $\times 455$ . Embryo-sac mother-cell of full size.
- Fig. 18. Longitudinal section of nucellus showing the row of four macrospores formed.  $\times 455$ . Of these the second will probably develop as the embryo-sac.
- Fig. 19. Longitudinal section of nucellus of older ovule.  $\times 455$ . The lowest segment of the mother-cell is developing into the embryo-sac.
- Fig. 20. Embryo-sac developing from the uppermost segment of the mother-cell.  $\times 455$ .
- Fig. 21. Two young embryo-sacs evidently derived from two cells of the tetrad.  $\times 455$ .
- Fig. 22. Group of antipodal cells from a mature embryo-sac.  $\times 680$ .
- Fig. 23. Egg apparatus from a mature embryo-sac.  $\times 680$ .

THE TRANSITION FROM STEM TO ROOT IN  
SOME PALM SEEDLINGS.

BY ERIC DRABBLE.

[TEXT-FIGS 4—10.]

SEVERAL anatomists have endeavoured to trace the changes in arrangement of tissues accompanying transition from root to stem in the seedlings of palms. The difficulty encountered lies in the fact that lignification of the sclerenchyma generally precedes that of the xylem, and the highly sclerenchymatous nature of the axis not only obscures the xylem, but also prevents satisfactory manipulation of the plants by the ordinary microtomic methods.

Van Tieghem<sup>1</sup> examined *Phoenix dactylifera* L. and came to the conclusion that it agreed with his "type I." That is to say, the number of xylem and phloem bundles in the hypocotyl is half the number in the root, the transition taking place by the branching of each internal xylem group to right and left of the phloem group external to it, the protoxylem of each branch turning outwards during the process. The phloem groups remain *in situ* hitherto; each now becomes separated from the next group by a pair of xylem branches with external protoxylem, which fuse to form a single group.

Miss Sargent<sup>2</sup> in the course of her extensive work on seedlings also examined *Phoenix dactylifera* and *Thrinax excelsa* and found evidence confirmatory of Van Tieghem's conclusions.

Certain palm seedlings recently examined do not entirely agree with Van Tieghem's description of *Phoenix*.

The difficulty of satisfactorily tracing the whole course of events is considerable, but the points referred to below have not been recorded without carefully examining a long series of seedlings of both *Phoenix dactylifera* and *Livistona mauritana*. My thanks are due to Professor J. B. Farmer, F.R.S., and to Dr. Chandler, for fully examining my sections and for giving help on doubtful points.

*Phoenix dactylifera* L.

Differentiation and lignification of the xylem elements set in late. In a seedling so young that the plumule is completely enclosed within the cotyledonary sheath, the tissues are as yet in the procambial condition, and it is quite impossible to trace with any degree of certainty the details of transition. It is necessary,

<sup>1</sup> Van Tieghem. *Traité de Botanique*.

<sup>2</sup> Sargent, Miss E. *Ann. Bot.* Vol. XVII., 1903.



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therefore, to deal with a plant in which the plumule has broken through the cotyledonary sheath, and grown out to some little length. A seedling at this stage is shown in Text-fig. 4. The primary

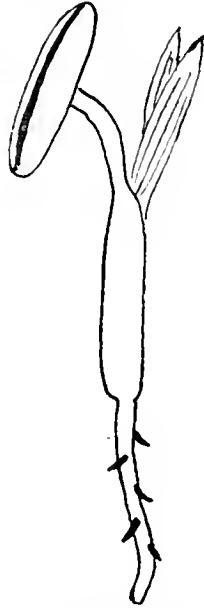


Fig. 4. *Phoenix dactylifera*.

root in such a seedling possesses about twelve xylem groups—the number varying from seedling to seedling. These xylem groups are for the most part independent of one another, and alternate with the phloem groups. The V-formation so often found in the large adventitious roots of mature palms is however occasionally present here also, the large metaxylem vessels of two bundles being approximated in such a manner that the two xylem groups form a V—the end of each limb being occupied by a protoxylem group, (Fig. 5 i.) At this stage the protoxylem consists of a few—three to six only—annular and spiral elements. As we follow the root upwards the metaxylem portions of the bundles are seen to be more and more united, and at the stage shown in Fig. 5 ii., there are four groups of metaxylem with respectively five, four, three and two protoxylem groups placed peripherally. At the same time the place of the large radially arranged metaxylem vessels is occupied by tracheids and vessels of a different character, resembling those of the stem-bundles. Following the root still further upwards, a gradual “splaying out” of the protoxylem groups is seen, and in many cases ground-parenchyma appears between the exarch protoxylem vessels and the metaxylem groups, (Fig. 5 iii.) The metaxylem elements just referred to as resembling those of the stem-bundles now give place to smaller elements, recalling in appearance the protoxylem of the typical root but having reticulately thickened walls.

At a slightly higher level the xylem groups are found to have approached nearer to the centre of the axis, while here and there traces of the protoxylem groups are seen to occupy a position near the periphery of the cylinder, widely separated from the more centrally placed main groups. These main groups are continuous with the "fused" metaxylem groups of the lower portion, and consequently with the individual xylem groups of the typical root, than which they are necessarily fewer in number—some six or

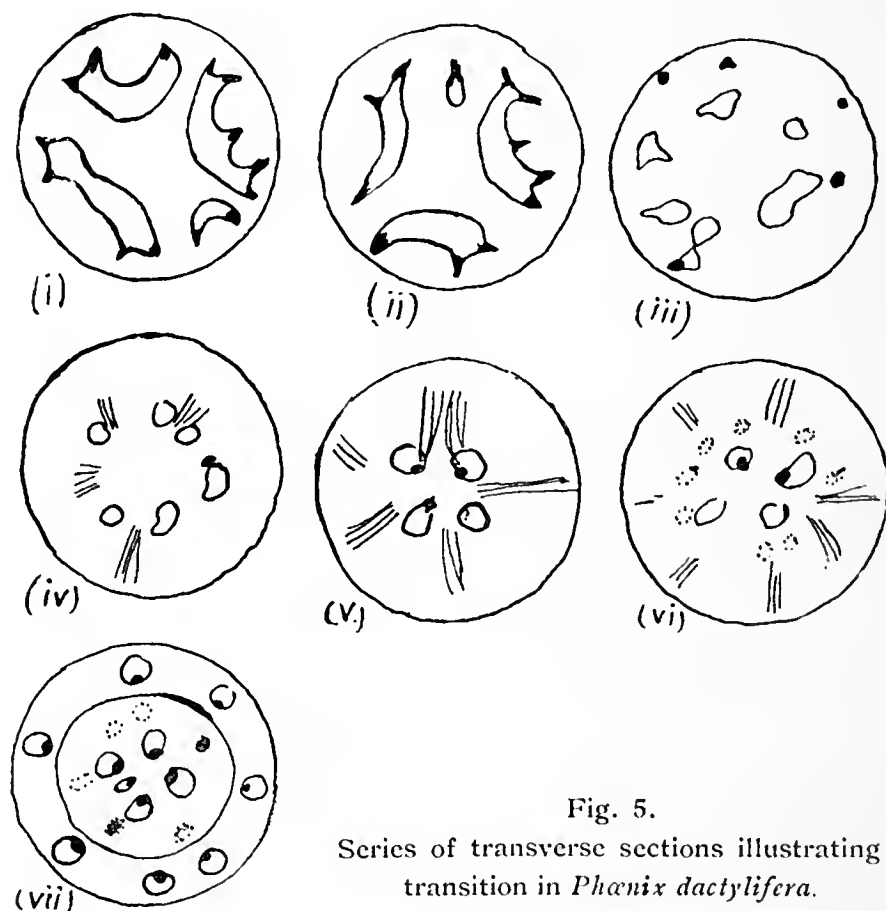


Fig. 5.  
Series of transverse sections illustrating  
transition in *Phanix dactylifera*.

seven being usually present. At about this level (Fig. 5 iv.) certain small elements appear in the xylem groups, which certainly seem to be protoxylem. The whole of the group is now composed of somewhat scattered elements, and these protoxylem vessels are more or less centrally placed. A little higher up the axis this protoxylem is found in an endarch position, and almost immediately above this the cotyledon bundles, of which there are six or seven, are seen running in an almost horizontal direction radially, (Fig. 5 v.) Each cotyledon trace is continuous internally with part of one of the axial xylem bundles. The rest of the xylem of the axial bundle is continued upwards into the plumule, which still shows very little differentiation of its tissues. The lower ends of the bundles—as yet in the procambial condition—supplying the first

leaf of the plumule, are now seen at the cotyledonary node. They are quite unligified and only partially differentiated (Fig. 5, vi.)

A little higher the cotyledon sheath with its six or seven bundles is separated from the plumule, which now contains the small but well developed upward prolongations of the root-bundles, continuous with the gradually differentiating and lignifying stem bundles (Fig. 5, vii.)

In order as far as possible to simplify the description of this somewhat complicated series of changes, the behaviour of the xylem alone has been considered. The phloem during the transition loses all connection with the xylem and runs in the form of more or less distinct strands in the parenchyma which separates the xylem bundles from the endodermis. Some of these are continued into the lower ends of the phloem bundles of the stem in the normal position of collateral bundles. Others are distributed to the xylem groups prolonged upwards from the root bundles into the cotyledon-stalk.

The bundles in the cotyledon sheath are multiplied distally by bifurcation, so that as many as twelve bundles may be found. The ground tissue at the base of the sheath, and also distally, is rather dense, but at a region about one third of the way up it is much more open, and round some of the individual bundles in this region a ring of cuticularized cells is found. Sometimes this ring is incomplete round the outside, *i.e.* externally to the phloem it is well developed, but internally, opposite to the protoxylem, it may be absent. A similar structure is found in *Livistona mauritana*, and is described at greater length under that heading.

*Livistona mauritana* WALL.

Only a fairly advanced seedling (Fig. 6) could be obtained. The cotyledon-stalk is very long and the sheath somewhat bulky. For convenience the structural changes will be traced from above downwards in this plant. A section at 5 (Fig. 6) shows the bundles scattered throughout the whole section of the cotyledon, (Fig. 8, i.) As many as fifty of these bundles may be present in this region. They are seen singly and in all stages of fusion with one another. Their function is that of conducting to the growing seedling the reserve food material, now rendered available in the soluble form by the ferments secreted in the cotyledon. In accordance with these functions but little xylem is present in the bundles. The phloem groups are well developed, and are enclosed in very dense sclerenchymatous sheaths. The bundles lie in a ground mass of typical parenchyma.

A section at 4, shows a similar arrangement of the bundles, but here there is a more extensive development of xylem, which is typically endarch in its arrangement. The phloem groups are frequently double, that is, two phloem groups may be found in conjunction with a single xylem bundle, and further fusion of bundles is seen to be going on. The fibrous sheath is somewhat less dense than at 5, and is relegated more particularly to the outer side of the bundle. The ground parenchyma is richly intermixed with lignified stone-cells—towards the periphery of the section these elements occur almost to the exclusion of all else. Amongst these are many mucilage cells containing bundles of raphides.

At 3, the number of bundles is further reduced to thirty-three, and the xylem is still very distinctly endarch. Some of the bundles show the double phloem groups, and the ground tissue is still provided with stone-cells, though somewhat less richly. Orientation of the bundles is frequently inverse, and fusions of bundles by their xylem portions are found, so producing a xylem-mass bounded both externally and internally by a phloem-group. The bundles are often roughly arranged in rings, the protoxylem of each bundle being orientated with reference, not to the centre of the cotyledon stalk, but to the centre of its own ring.

At 2, the number of bundles is reduced to sixteen. Many show double phloem-groups, and there is still indication of the grouping of bundles in sets round their own centre. The ground tissue is now almost entirely parenchymatous, and large irregular air spaces, similar to those described in the mature roots are present.

At 1, the number of bundles is reduced to nine. The xylem is fairly well developed, and the phloem is very abundant and arranged in a horseshoe-like form round the outside of each xylem-group. Some indication of the grouping of the bundles described above is still apparent, the protoxylems of all the bundles in any group converging towards one another as indicated in (Fig. 8, ii.) The ground parenchyma here encloses very large and extensive air-spaces. Surrounding each bundle is a layer of cells, some 3—4 elements in thickness with very thin and highly refractive walls, looking, under the high power of the microscope, as though they were cuticularized, but not responding to the endodermic test (iodine and strong sulphuric acid).

At 6, the arrangement of the nine bundles is almost identical; the grouping into three sets is however still better shown, and large and extensive air-spaces are present in the ground parenchyma. The sheath of small cells surrounding the bundle is here much as

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in the last section so far as its appearance is concerned, but on application of the endodermic test, a very distinct cuticularization of the walls becomes evident in the cells immediately external to the individual bundles, (Fig 7.) This cuticularization is of considerable interest as only occurring in that portion of the cotyledon stalk in which the large air spaces are present, being absent, both

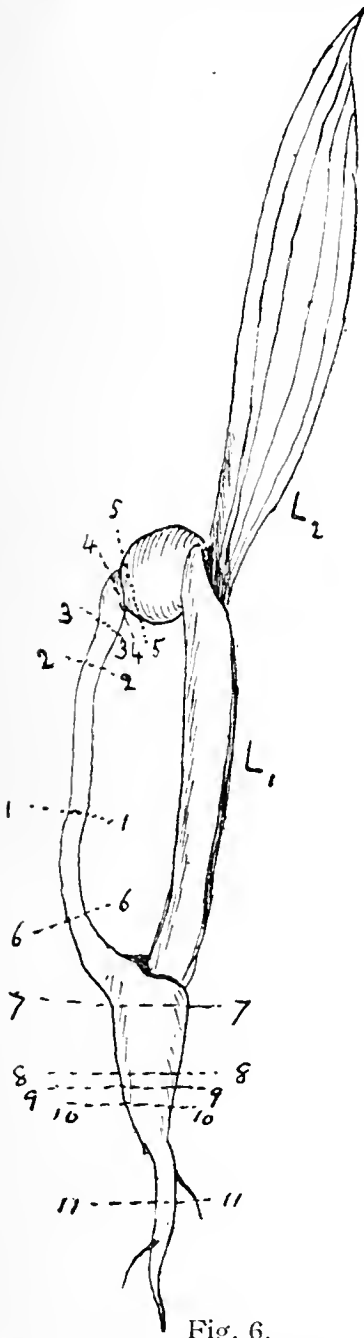


Fig. 6.

Seedling of *Livistona mauritana*.

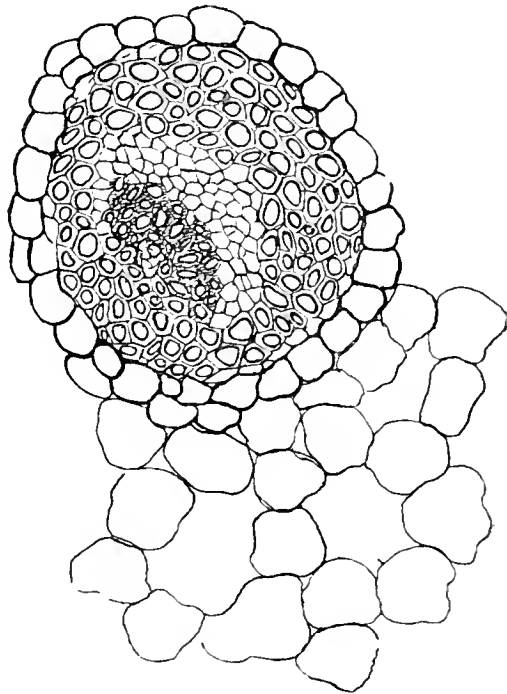


Fig. 7.

Bundle of *Livistona*-seedling  
showing endodermis.

above and below, where the ground tissue is denser. Just above the sheathing portion of the cotyledon stalk the bundles are reduced to a single ring of eight or nine (Fig. 8, iii.).

At 7, (Fig. 6), a section through the cotyledon-sheath shows nine bundles, seven of which are placed towards one side of the

cotyledon sheath, which is at this side expanded, while only two are found in the much attenuated and partly crushed tissues of the other side of the sheath. A ring of small but non-cuticularized cells surrounds each bundle, and it is interesting to notice that here the parenchyma is comparatively dense with but little air-space formation.

Of the two leaves found within the sheath of the cotyledon, the outer is richly supplied with typical bundles. The sclerenchymatous sheath is here greatly reduced as compared with that of the cotyledonary bundles. A striking point is that while the xylem and phloem are well developed in the more internally placed bundles, those placed more peripherally show all stages of reduction, until finally the peripheral ones consist solely of fibrous elements, which are larger in the centre of the bundle and closely resemble the vessels and tracheids of the true xylem in transverse section. Lignification is densest, and commences earliest in the peripheral fibres, and progresses internally in each bundle. Thus all stages between the typical bundles and the fibrous strands occur. Frequently some phloem elements are found after all true xylem has disappeared. A similar condition has been observed in the stem of a large tree of *Dictyosperma album*,<sup>1</sup> where many of the fibrous strands contain a few phloem elements. In this connection may be noted De Bary's statement,<sup>2</sup> recently confirmed,<sup>1</sup> that in the root of *Iriartia* occur strands of fibres with a central element appearing to be a sieve-tube, but not fully developed. The inner leaf is in a folded condition, and the tissues are but slightly differentiated. Lignification has, however, set in in a few of the bundles, commencing in an endarch manner. No trace of a cuticularized endodermis was anywhere found in this region, though the test was carefully applied repeatedly. All the parenchymatous tissues are here very dense.

At 8 the structure is essentially similar, but only eight bundles are found in the cotyledon sheath, (Fig. 8, v.) The parenchyma of the cotyledon sheath is here more richly supplied with air-spaces than at 7, and it is very interesting to find again that some of the bundles have extremely distinct sheaths of thin walled refractive nature, although cuticularization has not set in.

A section at 9 is closely similar, but the fibrous strands of the cotyledonary bundles are greatly reduced, and a third leaf is to be seen inside the second, (Fig. 8, iv.) The region between 10 and 11

<sup>1</sup> Drabble. *Anatomy of the Roots of Palms*. Trans. Linn. Soc., 1904.

<sup>2</sup> De Bary. *Comparative Anatomy of the Phanerogams and Ferns*.

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was worked for transition. Continuing down the axis, the three leaves are seen to merge into a central parenchymatous plumule, (Fig. 8, v.), with peripherally placed fibrous strands representing and continuous with, those of the outermost leaf. More internally is a group of scattered bundles, and it is quite possible to say in certain cases which bundles are distributed to any leaf. Lower down, the cotyledon-sheath is merged into the common mass, and

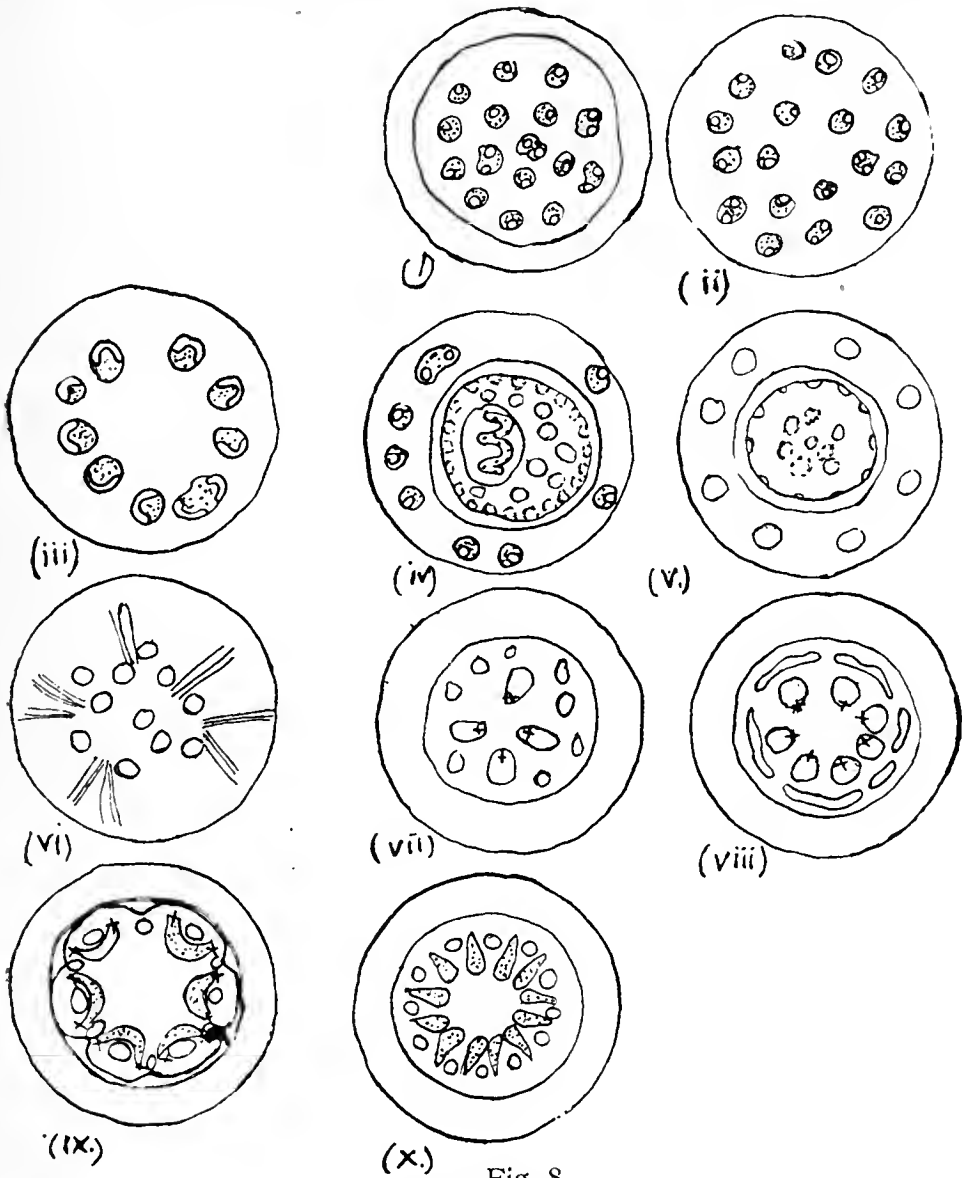


Fig. 8.

Series of transverse sections illustrating transition in *Livistona mauritana*. here the cotyledon-bundles run towards the centre of the axis, and lie in the common group of plumular leaf-traces (Fig. 8, vi.)

It is evident that here transition takes place between the root and both cotyledonary bundles and plumular bundles.

At the stage 4 larger and more centrally placed bundles represent the downward prolongations of pairs of cotyledonary bundles (Fig. 8, vii.) A little lower all the bundles which have shown numerous fusions among themselves become roughly

arranged in a ring, and the phloem loses all connection with the individual xylem-groups, and is found in a very irregular circle with numerous gaps, (Fig. 8, viii.), lying quite peripherally to the xylem groups. The xylem groups assume the form of a series of semilunar structures with the horns directed externally. About this stage the endarch protoxylem disappears, and a little lower protoxylem appears at the extremities of the horns, (Fig. 1, ix.), the change from the endarch to the exarch position being accomplished very rapidly. At the same time the phloem has taken the form of a continuous ring. These changes deserve a little more detailed consideration. Apparently what really happens is that in the upper regions of the hypocotyl and in the plumule and cotyledon, the lignification of the xylem commences in an endarch position and proceeds centrifugally, while in the root and the lower part of the hypocotyl it commences in an exarch position and proceeds centripetally. The downward extension of the endarch protoxylem and the upward extension of the exarch, do not appear to meet, nor do they overlap; and there is a very short region in the hypocotyl where there are no spirally or annularly thickened elements at all. This is just at the very slowly extending, or almost non-extending, portion of the hypocotyl, and it is not altogether surprising to find an absence of the kind of element adapted to rapidly extended regions. A similar state of affairs was observed by Miss Edith Chick<sup>1</sup> in *Torreya*.

Whilst these changes have been progressing the phloem ring has been broken up into twice as many strands as there are xylem groups; a phloem group now lies in the arms of each xylem V, and one between each adjacent pair of V's. These last named phloem groups are accompanied externally by an inwardly projecting sclerenchymatous mass of pericyclic fibres (Fig. 8, ix.) At first sight the impression that the phloem groups opposite the fibrous masses have been pushed centrally by the development of the latter is very strong, but there is no histological evidence of any crushing of the tissues in their neighbourhood.

Lower down the xylem V's become discontinuous centrally, and thus a phloem group alternates radially with each xylem group and the typical root-structure is attained.

#### *Oreodoxa regia.*

The mode of transition is essentially similar to that in *Livistona mauritana*, but the central cylinder has ground-tissue of so densely lignified a character that it is more difficult to trace the

<sup>1</sup> Chick, Miss E., NEW PHYTOLOGIST, Vol. II., pp. 86—88.



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changes in the xylem groups. Careful comparison of several series of sections has, however, rendered the main points clear.

*Pritchardia* sp. (Fig. 9).

The transition is in all respects similar to that in *Livistona mauritana*. The ground-parenchyma of the cotyledon stalk and sheath is throughout dense, and no trace of a cuticularized ring round the bundles was anywhere observable.

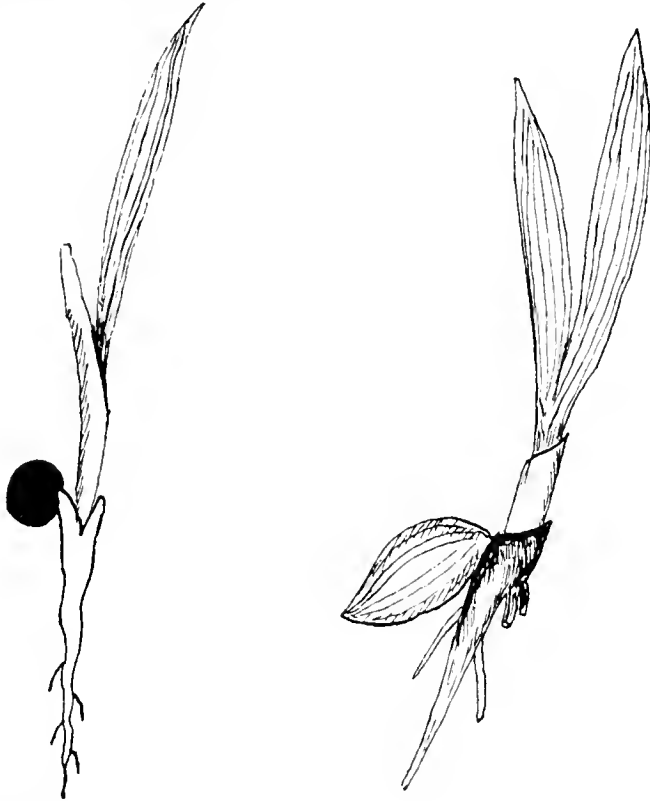


Fig. 9. *Pritchardia* sp.      Fig. 10. *Coleospadix* sp.

*Coleospadix* sp. (Fig. 10).

The transition appears to be of the same type, but the very short curved stalk of the cotyledon, and the advanced age of the seedling rendered examination very difficult.

Two points brought out above require a little further consideration.

In the first place there is the question of the cuticularized layer surrounding some of the bundles in the cotyledon stalk of *Phoenix dactylifera*, L. and *Livistona mauritana*. This sheath in its cuticularized state can only be detected in that short portion of the stalk where there is a rich development of air-spaces. That the function of the endodermis is to cut off the bundles from the external air has long been suspected. The rich development of aerenchyma in the roots of many aquatics is frequently accompanied by the presence of a well-developed endodermis, and indeed

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the rôle of an air-tight sheath allotted to the endodermis by many physiologists seems to be well supported from the anatomical side.

It is with the xylem portion of the bundle that this function of the endodermis is generally assumed to be associated. This however, is not very clear. In roots the endodermis may be provided with non-cuticularized "passage cells." These cells occur opposite the xylem groups, while the cuticularized elements are usually continuous over the phloem regions. The frequent reduction of xylem in aquatic plants is not necessarily, or even generally, associated with reduction in the endodermis.

In *Phoenix* and *Livistona* the endodermis-like sheaths to the cotyledonary bundles are frequently incomplete, being wanting on the xylem face, though present on the phloem face. Again, in ectophloic medullated monosteles the presence of an internal endodermis between xylem and central parenchyma is rare; on the other hand when an amphiphloic condition obtains, an endodermis often cuts off the internal phloem from the central parenchyma. It is conceivable that the endodermis may find its function rather as a phloem sheath than as a xylem sheath. This is at all events possible. Further investigation alone can support or disprove the validity of this suggestion.

There appears to be true transition between the bundles of the root and, on the one hand, those of the cotyledon, on the other those of the stem. In Monocotyledons it is generally found that the continuity is primarily between the root- and cotyledon-bundles only, and that the plumular traces are secondarily inserted upon these common strands at, or below, the cotyledonary node. In the palm seedlings examined, it is true the plumular traces are later in differentiation and lignification than the cotyledonary bundles. This is to be expected, seeing that the cotyledonary bundles serve as conductors of the elaborated food-material from the seeds to the growing seedling. At the same time, however, some of the xylem and phloem strands of the root are directly and primarily continuous with those of the plumule, and have no connection, or only a *lateral* one, with the strands common to root and cotyledon.

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OCCASIONAL NOTES.

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PLANT DISTRIBUTION.

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THE THIRD TANGANYIKA EXPEDITION.

In *Nature* of January 25th appears a brief account by Mr. W. A. Cunnington of his recent expedition to Lake Tanganyika, undertaken largely in order to ascertain whether the botanical evidence bears out the striking conclusions arrived at by Mr. J. E. S. Moore on geological and zoological grounds.

Water weeds, algæ and phyto-plankton were collected from Nyassa, Tanganyika and Victoria Nyanza. Of the first named we are told that the Tanganyika forms appeared to differ but little from those collected in Nyassa.

The working out of the collections will be awaited with much interest.

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PLANTS OF THE SEYCHELLES.

In the same issue of *Nature* there is an interesting letter from Mr. Stanley Gardiner on his recent visit to the Seychelles Archipelago. Little indigenous jungle remains in the islands, but most of the trees are endemic species or genera. The more open spots in the forests have a dense undergrowth of Ferns, Lycopods, Selaginellas and Psilotum which cover also the lower parts of the trees. There is a comparative absence of herbaceous dicotyledons. The angiosperms shew a sharp distinction unto calciphilous, siliciphilous and "indifferent" types, the last-named being a smaller percentage of the whole than either of the other two. Most of the calciphilous plants are identical with those of other coral islands visited and were probably ocean borne.

*Lodoicea seychellarum* has, according to Mr. Gardiner, two distinct, structurally different types of nut borne in about equal proportions on the same female trees.

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MR. GUPPY ON PLANT DISPERSAL.

We have received from Messrs. Macmillan & Co. Mr. H. B. Guppy's work, embodying his researches of more than twenty years on Plant Dispersal, particularly by ocean currents. We shall shortly publish a detailed review of this important work, but may note here one of Mr. Guppy's main conclusions. He holds that the *whole* of the structural peculiarities which enable littoral seeds and fruits to float, are antecedent to the adoption of the floating habit, and are thus to be regarded as non-adaptive characters.

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“THE ORIGIN OF GYMNOSPERMS” AT THE LINNEAN  
SOCIETY.

AT the meeting of the Linnean Society on Thursday, March 15th, the evening was devoted to a discussion on the “Origin of Gymnosperms.” There was a very full gathering of botanists, including several who had come to London specially. The discussion was to have been opened by Addresses from four Fellows, Professor F. W. Oliver, Mr. E. Newell Arber, Mr. A. C. Seward and Dr. D. H. Scott, each dealing with the subject from a somewhat distinct standpoint. Abstracts from these addresses were prepared and circulated beforehand. In the event, the first three addresses lasted from 8.20 till 10.5, occupying about 35 minutes each. At the close of Mr. Seward’s remarks, the President suggested that the fourth address (Dr. Scott’s) and the general discussion should be deferred till the next meeting on April 5th.<sup>1</sup> This proposal was accepted by the meeting. It has been thought that a full report of this discussion would be of considerable interest, and permission has been kindly given by the Council of the Society, and by the Openers, for this to appear in *THE NEW PHYTOLOGIST*. The speakers have been good enough to revise the proofs of the reports of their respective addresses.

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PROFESSOR OLIVER, in opening the subject of discussion from the more general stand-point, said that in the old days before the situation arose that gave point to one aspect of to-night’s discussion it was always supposed that the relative abundance of fossil remains of Vascular Cryptogams at any geological period shewed a rough correspondence with its age. As one went back, first one and then another group of seed plants died out, till there remained only the gymnospermous phylum of the Cordaitæ which lost itself in the Devonian rocks alongside of Pteridophytic forms from which, or in common with which, it, and the other seed plants, might have taken origin.

This conception of the relations in the remote past was quite consistent with the results of the Hofmeisterian School of Morphologists, which pointed to a passage of Vascular Cryptogams into seed-bearing plants.

The inevitable oscillation of views as to the immediate affinities of the Gymnosperms had not in any way undermined the Hofmeisterian position. Whilst both the ferns and the lycopods had successively found favour in this connexion, the current of opinion had latterly set strongly in favour of the ferns. Those who were conversant with recent advances in fossil-botany are aware that good reason had been found to transfer, wholesale, plants once supposed to be Cryptogamic to the status of seed-bearing plants. He would illustrate the general nature of these plants, which included the bulk of the carboniferous “ferns,” by special reference to *Neuropteris heterophylla*, *Lyginodendron oldhamium* and *Medullosa anglica*. Fern-like plants such as these, that bore seeds, it was

<sup>1</sup> This date was subsequently altered to May 3rd,

convenient to call Pteridosperms. Their number was increasing every day and, according to some estimates, they threatened to deplete the true ferns entirely. If the coal-measure ferns were thus turning out to be something else—if the much respected ancestor were nothing but a sort of ghost and never had a substantial existence—then a situation arose which might well engage their attention. He trusted that to-night's discussion might be reassuring. The discoveries alluded to did not come as a bolt from the blue. A great stride had been made more than ten years before, when examination of petrified material shewed that certain palæozoic fern-like types (notably *Lyginodendron*) had many of the anatomical characters of the Cycads. These had become known as the Cycadofilices, but their mode of reproduction, whether "cryptogamic" or spermatophytic, had been entirely unknown. The recognition of the Cycadofilices, a transitional group, had pointed to the origin of the Gymnosperms from an old Filicinean stock, but it had not really shaken the old position, for after all, relatively few, in proportion to the total number of ferns recognised, were preserved in the form of petrifications. But in the sequel, when first one, and then another of these forms turned out to be seed plants and the hosts of fossils preserved as impressions became available, the situation was altered. For, structure-work having played its necessary preliminary part, here was a criterion which could be demonstrated from impressions with perfect validity; and day-by-day the big battalion of Ferns was being depleted and Pteridosperms set up in their stead. The whole of the Sphenopterids and Neuropterids must be removed from their reserves of Ferns. He would call attention to a chart which shewed in a general way this distribution in time of the main groups of vascular plants. Cordaites went back as far as any fern-like forms.

Among the Ferns which still remained the Pecopterideæ were under suspicion. One of them, *Pecopteris Pluckencti*, had been caught by M. Grand'Eury in the delinquency of producing a multitude of seeds. Anatomically, too, the group was somewhat complex, and not very suitable as the starting point of Gymnosperms. Some might incline to look to the Lycopod phylum for a way out. Mr. Seward would tell them the conclusions he had reached from a detailed study of the Araucariæ, plants in habit certainly recalling the Lycopods. He (Professor Oliver) would shew them two lantern slides of seedling Araucarias which certainly brought this resemblance out very strikingly. Mr. Seward's contribution would be a very special feature that night, and should he find reason to suspect the existence of a sort of Conifero-Lycopod series parallel with the old Cycadofilices on the fern side, he might try to drive home his Lycopod "wedge." In any case Mr. Seward had chosen the right tactical moment for bringing forward his views. Yet the Cycads and Pteridosperms pointed clearly enough in the direction of Ferns, and one turned to one group among the latter not yet suspected of the seed-bearing habit. He alluded to the Botryopterideæ. Mr. Arber would probably draw particular attention to this group. He (Professor Oliver), believing that Mr. Arber held a good hand, was tempted to lead a card into his strong suit. The Botryopterideæ were an obscure collection of forms to most of them till they were focussed in the pages of Scott's "Studies." The potentialities of the group were first recognised in that work. They

were an old generalised or synthetic group, having much in common with archaic living ferns. Under other circumstances one might feel a trespasser, but Dr. Scott was like a kindly landowner who admitted others to the park which he had planted. He would draw attention to the Botryopteridæ in one connexion only. The Pteridosperms included forms with a wide anatomical range. There were solid monostelic forms (*Heterangium* and *Suteliffia*), medullated monostelic types (*Lyginodendron*) and complex polystelic forms (*Medullosa*, *Cladoxylon*, etc.), in which each several stele is a centre of secondary thickening. Now it was a remarkable fact that among the Botryopteridæ there were represented vascular stem structures which might well serve as a starting point for the evolution of these different Pteridospermic types, as he would shew them by means of lantern slides. His view was that a great period of vegetative development was inaugurated among these archaic ferns in, perhaps, the Devonian epoch, and that this was correlated with a greatly increased demand for vascular tissue in the stem. This crisis had been met by an expansion of the primitive stele, sometimes limited, sometimes so violent that the verge of fragmentation was passed and the original stele split up into a number of parts. They would see by comparing the diagrams shewn that the *Lyginodendron*-type, the simple *Medullosa*-type and the *Cladoxylon*-type could easily be derived from different forms of Botryopterid stele. The roots of Palms were instanced to illustrate the power of plants to fragment their steles under certain conditions. This suggestion, brought forward now in its crudest form, could not advance to the rank of a definite theory till the questions of leaf-traces and protoxylems had received a searching scrutiny. In conclusion he would say that he was in sympathy with the general position laid down in Mr. Arber's abstract. The Botryopteridæ seemed to be the relics of a big generalised group of Cryptogamic plants, and contained the potentialities of evolution along many lines. In his opinion the fern-like plants remaining after all Pteridospermic deductions were adequate for the derivation of all the groups of seed plants, though these might have come off at very different epochs. There was only one more point he would raise. It was possible they were inclined to exaggerate the extent of the Pteridosperms. No doubt whole groups of Ferns had broken away from the Botryopterids, but might not others lie masked by the Pteridosperms. In the Lycopod phylum they knew they had *Lepodendra* with *Lepidostrobus* fructifications and others with the *Lepidocarpon*-type. The former were true Cryptogams, while the latter had several of the characters of seed-plants. To a certain extent the same thing was true of living Selaginellas. Was it not possible that, on the Filicinean side, our *Heterangiums*, *Lyginodendra* and *Medullosæ* might be accompanied by purely cryptogamic species of like habit, but not necessarily heterosporous, whose real nature was masked by the recent discoveries of Pteridosperm seeds? They would gather that he was inclined to a conservative view of the position, to depend still upon a cryptogamic group for the origin of the Pteridosperms and eventually of the Cycads and Cordaitæ. And if of the Cordaitæ, then they were logically bound to include the Conifers as well, though the origin of these last was, of course, obscure, since their early forms had not been discovered in the petrified condition.

MR. E. A. NEWELL ARBER, whose address was entitled "The Earlier Geological Record of the True Ferns," said, that any consideration of the origin of Gymnosperms must also involve a consideration of the ancestry of modern ferns, since, as was evident from Professor Oliver's remarks, the two groups had a common origin far back in the Palæozoic epoch. His remarks would be confined to the Filicinean line of descent. Within the last three years so great a light had been thrown on the nature of the reproductive organs of the Pteridospermeæ, that a correspondingly deep shadow had been cast over much of the available evidence for the existence of the Palæozoic ferns. Anyone who had looked over museum collections of Carboniferous fossils or had collected on the tips or heaps at the mouths of coal-pits, would be aware of the fact that impressions of these ferns or fern-like plants were both numerous and varied. All such fossils had, so to speak, been collected into a great lucky-bag, from which we had, during the past few years, been helping ourselves with both hands. Every specimen hitherto drawn had proved, or was suspected to belong to the Pteridospermeæ, so that now we were faced by the question, are there any true Palæozoic Ferns? Are they all at the bottom of the bag? Did they exist at all? This situation had led to what Dr. Scott, in his abstract, had described as being of the nature of a "scare." Such a scare might perhaps be regarded as amusing, when it was remembered that after all there is ample evidence from the foliage and anatomy of the known Pteridosperms that they themselves must have been derived from Fern-like Ancestors. Where, then, were these Ferns? It behoved us to search very carefully the older Mesozoic and the Palæozoic records, and we should probably do well to distinguish, during our search, between the Leptosporangiate and the Eusporangiate types. There was ample evidence that in the Triassic, Jurassic and Cretaceous periods the Leptosporangiate Ferns had attained to the position of a dominant type, and that all, or practically all, of the modern Leptosporangiate families had been differentiated out during the Mesozoic epoch. But if we tried to trace these back to Palæozoic times, we were met by difficulty. In fact he doubted very much whether Leptosporangiate Ferns, in the modern sense, existed at all in the Palæozoic rocks. We had the Botryopterideæ and also a fair number of fronds hitherto unassigned, but bearing annulate sporangia. The structure of these sporangia however, did not agree in details with those of the present-day Leptosporangiatæ. The annulus was always bi or multi-seriate, in opposition to the uniseriate type of the modern forms. It was helpful in our present difficulties to regard the Palæozoic Ferns as an ancient race combining the characters of both Lepto- and Eu-sporangiate forms. This was not a new idea, since it had been foreshadowed by Scott in his "Studies" (1900). For this ancient synthetic race, he (Mr. Arber) proposed the name of *Primofilices*. Such names as Palæopterideæ and Archæopterideæ, in many respects preferable, were unfortunately barred by the existence of the form-genera Palæopteris and Archæopteris. On one point the geological record was emphatic as regarded the Filicinean line of descent. Whether we regarded these Palæozoic Ferns as members of an ancient race, the Primofilices, or as true Leptosporangiate forms, in any case they were not one of the

dominant or ruling groups in Palæozoic times. The Botryopterideæ were the only family of Primofilices that had been clearly defined. He proposed to leave in abler hands the discussion of the connexion between the Botryopterideæ and the modern Leptosporangiatae. He would however call attention by means of lantern slides to the sporangial structure of the Botryopterideæ, which clearly did not agree in detail with that of a modern Leptosporangiate fern.

It was, however, with the Eusporangiatae, that he would be chiefly concerned that night, because it presented special difficulties. Did they exist in the Mesozoic? Did they exist in the Palæozoic? If so, what was their relationship to the Leptosporangiatae? These were problems which were necessarily pushed to the front by the progress of contemporary research. If we search the records, can we find any period in which Eusporangiatae had attained the dominant phase? The life-line of a group of plants could, in his opinion, be represented by a lenticular figure stretching through, perhaps, several periods of the world's history, the breadth of the figure at any point being proportional to the number and variety of the forms existing at that time. With regard to the Ophioglossaceæ, there was no good evidence at all of their existence either in Palæozoic or Mesozoic times. He knew of no fossil put forward as a possible representative of the Ophioglossaceous type, which would to-day be regarded as trustworthy evidence of the occurrence of that family. Such evidence as we had related rather to the other Eusporangiate family, the Marattiaceæ. In older Mesozoic rocks, such as the Rhætic, a very few examples could be recalled. *Tæniopteris* was one of these. *T. Münsteri*, a typical Rhætic plant, bore synangia closely comparable with those of *Marattia*. *Dauæopsis* had compound fronds whose pinnae were like the whole frond of *Tæniopteris*, and in some cases the synangia resembled those of the recent *Dawsonia*. But there was a suspicion that *Tæniopteris* might be the frond of a Cycad bearing microsporangiate synangia. At any rate, whether these plants were really Marattiaceous or not, there was certainly no evidence that the Eusporangiatae were a dominant group in the Mesozoic. In the Palæozoic rocks, however, we did find a plexus of plants which had for many years been regarded as being true Eusporangiate types. These were the Pecopterids, which had exannulate sporangia, either independent or united to form synangia. What was their precise nature? Were they true homosporous ferns, or were they male fronds of Pteridosperms? To this question we could give, at the moment, no decided answer. He was inclined to think, however, that the latter alternative was the more likely. There were three points of great significance in this regard. First there was the discovery that *Pecopteris Pluckenetii* was seed-bearing, and although it was not quite a typical *Pecopteris*, this seemed no sufficient reason for dissociating it from the group. Secondly there was the recent discovery by Mr. Kidston of the microsporangiate organs of *Lyginodeudron*, which were exannulate fern-like sporangia. Thirdly there were the Bennettitæ, the microsporangiate fronds of which were very Marattiaceous-like in structure, the microsporangia being united into synangia. If this were so, how much more likely was it that the Pteridosperms themselves, the direct ancestors of Bennettitæ, should have had similar microsporangiate fronds. He would exhibit a lantern slide shewing typical Pecopterid leaflets bearing synangia. He now came to *Psaronius*, a



Palæozoic stem, of tree-fern habit, shewing structure, and would shew by means of lantern slides its well-known and very Marattiaceous anatomy. This was the best evidence that could be offered in support of the view that Eusporangiate Ferns existed in Palæozoic times. Some species of *Psaronius* bore Pecopterid fronds with synangia. Nevertheless he was not quite sure that *Psaronius* was really an Eusporangiate fern. It was just possible that a principle which we were too apt to lose sight of might apply here. Among recent plants what he had called *homœomorphy* was very frequent, as everyone admitted, and it could certainly also be detected among fossils. That two plants belonging to two quite different lines of descent might have acquired very similar morphological features was certainly true. He might refer to the Palæozoic seed plants, *Cordaites*, which Professor Oliver had mentioned. No one would now argue that because the Cordaites and Pteridosperms both bore seeds a direct connexion existed between them. In the Palæozoic period, forms on more than one line of descent had attained to that particular form of heterospory which we called a seed, but that fact was no evidence of close affinity between the forms in question. It seemed possible that the resemblances between the microsporangiate synangia of Palæozoic Pteridosperms and the synangia of modern Marattiaceæ may also be simply due to parallism of development. However that might be, he could find no evidence that in the Palæozoic epoch, Eusporangiate forms had attained a position of dominance, whether the Pecopterids bearing synangia were really Eusporangiatæ or otherwise. Two practical points emerged from this discussion. We should use every endeavour to determine the precise nature of the Pecopterids of the Palæozoic rocks, and we should pay particular attention to the Botryopterideæ and to the other families of Primofilices which would probably become separated out in the near future.

MR. A. C. SEWARD, rising at 9.30 to speak on the Araucariæ and the origin of Conifers, felt there was some danger that evening of the different speakers attending too exclusively to their own aspects of the subject and neglecting to discuss the views put forward by others. He would have liked to criticise some of the statements of previous speakers with which he had found himself unable to agree, but he had been instructed to confine himself to one particular text, which concerned the Conifers. In discussing the evolution of Gymnosperms they were mainly concerned with the Cycads and Araucariæ. He contended that those who accepted the view that Cycads were derived from Ferns had gone too far in including the Conifers in the Fern-Cycad alliance. He held the view that Conifers, or at least some of them, might have been derived from the Lycopods. He would confine himself mainly to the Araucariæ, which, while they could not be removed from the Conifers, constituted in many respects a group apart. One question which had to be asked in considering the phylogeny of such a group—was whether the Araucariæ were an old group of Coniferæ. So far as the evidence was before them the Araucariæ were certainly an old group. Probably no group of Conifers existing at the present day could trace their descent further back. Recently some botanists had stated with a certain dogmatism that

the Abietinæ were older than the Araucariæ. So far as the fossil evidence went there was no support at all for such a view. A case on which some stress had been laid was Nathorst's example of an Abietineous cone from the Rhætic. If one examined Nathorst's figures one was forced to conclude that by itself this cone is of practically no value as evidence of the antiquity of the Abietinæ, and the view of the geological age of the Abietinæ rested almost entirely on evidence of that kind. They might now turn to the Araucariæ. The fossil evidence on which they might rely to establish the age of a group was of three kinds, petrifications shewing structure, impressions of twigs, etc., and lastly, and most important, impressions of cones, *i.e.*, of the reproductive organs. In the Palæozoic rocks they found an abundance of petrified wood so like that of the modern Araucariæ that it might be said to be identical with it. Much of this, however, was really Cordaitæan. And in many cases the difficulty of determining whether such wood really belonged to Araucariæ or to Cordaitæ was practically insuperable. The occurrence of this wood did, however, shew that this was a very old type of wood, to whatever plants it belonged. In the lower Mesozoic also, such as the Liassic of Whitby, there was some abundance of Araucarian wood. The Palæozoic impression *Volkia* described by Renault from the Permian, bore rather a striking resemblance to a modern *Araucaria*. Sometimes, even, it had reproductive shoots with monospermic cone-scales. Also Araucarian wood had been found in connexion with the *Volkia* impressions. Hence we were perhaps justified in assuming a relationship here, and probably also in the case of *Pagiophyllum*, whose twigs, abundant in the Liassic, were externally like those of *Araucaria*. These pieces of evidence taken together had weight, though they were not perhaps conclusive individually. In the Mesozoic rocks, particularly the Jurassic, Araucarian cones were by no means uncommon. They were found in India, Australia, Britain, France and other parts of the world. Some were very well preserved and agreed in important respects, such as the broad scale, its narrow membranous margin, and the single seed, with modern Araucariæ. There could, then, be very little doubt that the Araucariæ were very abundant and widely distributed in the earlier Mesozoic, certainly far more so than the Abietinæ. If they granted the age of the group, were the Araucariæ also primitive? He ventured to maintain that they were. One character which suggested primitiveness was the very gradual transition from the ordinary foliage leaves to the sporophylls. This could be seen from the lantern slide shewn in *A. Mulleri* and *A. Cookii*, and the same was true of the female cone of *A. imbricata*, the Monkey-puzzle. It was certainly not the case in many other Coniferæ. Then the question arose whether there were primitive anatomical characters in modern Araucariæ. The wood was uniform and simple and consisted almost entirely of tracheids with multiseriate bordered pits on their radial walls. There was also no xylem parenchyma that he could find, and Professor Penhallow of Montreal, who had carefully investigated the genus, agreed in that view, though contrary statements had been previously made. There was another character of Araucariæ, to which Sir W. Thiselton-Dyer had recently called attention, and that was the persistence of the leaf-traces in the wood even of trunks which might be as much as fifty years old. He would illustrate this

by a lantern slide which shewed a trace cut across in a tangential section of the wood. Such leaf-traces must have long ceased to be of any use to the plant. In this respect *Araucaria* appeared to resemble the Palæozoic Lycopod *Lepidodendron*. The relationship between the reproductive organs of *Araucaria* and the Lycopods was a vexed question. There was certainly little or no resemblance between the male sporophylls of *Araucaria* and the corresponding structures in Lycopods. But the Araucarian male flowers did recall the cones of *Equisetum* and of *Cheirostrobus*. This last form was a generalised type combining the characters of Equisetaceæ and Lycopods, and thus could be regarded as forming a link between *Equisetum* and *Araucaria*. With regard to the female cones of *Araucaria* he ventured to hold that the individual scales were single sporophylls, each homologous with a foliage leaf. Between the ovule and the distal end of the scale one found, as he would shew on the screen, a small outgrowth, called as a matter of convenience a "ligule." On the scale of *Agathis* there was a very slight prominence corresponding in position with the more conspicuous ligule of *Araucaria*. It had been rather the fashion in recent years to consider the cone, of the pine for instance, not a flower, but an inflorescence; and each cone-scale a reduced axillary shoot in the axil of a subtending bract. This view had become so firmly fixed in the minds of many botanists that they had gone rather out of their way, he might say indeed very considerably out of their way, to bring all the other Conifers into line with it. But if *Araucaria*, for instance, was so much older and more primitive than the Abietineæ, as he had endeavoured to shew that it was, why should its cone be interpreted in the light of the specialised *Pinus*? Even if the axillary shoot theory were true of the Abietineæ, he maintained that it was not true of the Araucarieæ. Could they now find indications of primitiveness in the structure of the ovules themselves? There were a greater number of archegonia than in most Conifers, and they were scattered irregularly in the prothallium, as he would shew them on the screen; the same was true of *Sequoia*. This character might also be primitive. Some of these archegonia, too, did not communicate directly with the surface by means of a neck, and this was also true of *Sequoia*. They might now turn to the reasons which had led botanists to believe that the Conifers belonged to the Fern-Cycad stock. He ventured to consider those reasons wholly insufficient. One of them depended upon the Cordaitæ. The leaves of *Cordaites* were not unlike those of *Agathis* and the wood was practically identical with that of *Araucaria*. It had been generally assumed that that meant relationship, but the evidence appeared to him not to be good enough. The leaf-form clearly alone might be valueless as evidence. They all knew many cases of plants of widely different affinity in which the leaves were externally very similar. The internal structure of the leaves of the Araucarieæ was, as a matter of fact, decidedly different from that of *Cordaites*. In the reproductive organs there was very little resemblance. He would admit that the axillary shoot theory, if applied to *Araucaria*, might furnish a point of contact with *Cordaites*, but this he submitted was deliberately reading complexity into simplicity. Some years ago certain petrified stems had been described, from lower Carboniferous strata, in which strands of primary wood occurred at the edge of the

pith, as in *Lyginodendron*, the secondary wood being like that of *Cordaites*. The argument was that this character brought *Cordaites* into relationship with the Cycadofilices, and that the Araucariæ were so like *Cordaites* as to bring them into the same circle of affinity. But this evidence was insufficient. They had yet to demonstrate a relationship between the reproductive organs of Cordaitæ and Araucariæ. Finally, if they were not willing to accept the Fern-Cycad view of Araucarian affinity, what was the evidence for a Lycopod ancestry of the Conifers, or at least of the Araucariæ? He would leave the question of habit out of consideration. Prof. Oliver had spoken of the resemblance of habit, but perhaps he had merely dangled that as a bait. Let them take the wood. There were obvious differences between the structure of the wood of Araucariæ and that of the Lycopods. The former had multiseriate bordered pits on the tracheid walls, while the latter had scalariform pits. This was of little importance because they all knew plenty of instances where there were transitions between scalariform and “pitted” tracheids in the same plant. Another point was the absence of the centripetal xylem, conspicuous in Lycopods, from the stem of the modern Araucariæ. But there was a considerable amount of transfusion tissue in the leaves of *Araucaria* and *Agathis*, and that might perhaps be homologous with centripetal xylem. But, as Dr. Scott had pointed out in “The Old Wood and the New,” there was a strong tendency among plants which had adopted the method of producing centrifugal xylem by means of a cambium, to give up centripetal xylem altogether. So that this difference in the stems of the two groups was no evidence of want of relationship. As regarded the male cones, they could not point to any close agreement between the Araucariæ and the Lycopods, though as he had pointed out *Cheirostrobis* might be regarded as furnishing a connecting link. As regarded the female flowers the single sporophylls bore a strong resemblance to those of *Selaginella* and *Lepidodendron*. One striking point of difference was the fact that modern Lycopods did not produce any seeds. But they had *Lepidocarpon*, which fulfilled most of the characters of a true seed. Indeed it suggested comparison with the Araucarian seed because neither had a pollen-chamber and both were therefore of distinctly different type from those of the Pteridosperms and Cycads. This was an important argument in support of the view that the Lycopods might be the ancestors of the Conifers. He was afraid he might have been guilty of unbecoming dogmatism in the statement of his case, but he thought it important for the sake of discussion that each speaker should state his view as clearly and definitely as possible. He must reiterate his view that in any case the evidence for the derivation of the Conifers from Fern-like ancestors was wholly insufficient.

[The Discussion was then adjourned.]

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ON ABNORMAL FLOWERS OF *SOLANUM TUBEROSUM*,

BY DAISY G. SCOTT, B.Sc.

WITH TEXT-FIG. 11. [I.—VIII.]

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THE flowers described in this note were gathered in August 1897, by Professor Harvey Gibson, in a field near Cuilimuich Farm, Carrick Castle, N.B. The farm lies on a river delta, composed of alluvial soil, which had been cultivated for generations.

Each of the flowers examined shewed some abnormality. A curious feature found in all the flowers was the presence of ovules in large numbers on the filaments of the stamens, notwithstanding that the ovaries in the same flowers produced normal ovules in the usual fashion. In some of the flowers, although the full number of fertile stamens was present, one or two of the petals were found with well-developed pollen-sacs containing pollen-mother-cells, which in one instance had reached the tetrad stage.

The flowers had the usual number of parts, not a single instance of abortion being seen. Only in one case was increase in number of parts found, namely where in one flower the ovary was evidently composed of three carpels, and possessed three loculi.

Sections taken from the distal part of the flower-bud shewed five stamens alternating with the petals, and a two-celled ovary with axile placentation. At this level the flower appeared to be quite normal. The pollen-sacs and tapetum were well-developed, and numerous pollen-mother-cells occurred in the loculus. Sections taken at a lower level, however, shewed on the ventral face of the stamen, *i.e.*, on that side directed towards the ovary, the presence of two or three ovules. These ovules were fully-formed and differed in no respect from those found in the ovary. They were anatropous and had developed fairly large embryo-sacs. Sections taken quite near the base of the flower shewed numerous ovules

on the stamens, springing from the tissue facing the axis of the flower. They covered the whole available surface on this side of the stamen, and were scattered about without any apparent order. The transverse sections generally cut the ovule longitudinally, thus allowing the embryo-sac and integuments to be clearly seen. Often however the ovules did not grow out at right angles to the axis of the stamens, but were directed obliquely upwards, (Fig. 11, I). Another curious point in those sections was that many ovules cut in various planes appeared to lie freely in the space between the ovary and the stamens. This effect is explained by the fact that just below this level the stamens suddenly bulge out to form a ridge. This ridge, like the whole interior face of the stamen at this level, was covered with ovules, many of which shewed no connexion in transverse section with the stamen on which they grew.

In the flower under consideration four of the stamens shewed the peculiarities described, the fifth producing no ovule on any part. It exhibited one peculiarity however, namely, that it was partially petaloid (II), being flattened out very much laterally. The anther lobes were no longer distinct from the connective, and the whole structure appeared in transverse section the same thickness throughout. At both ends pollen-sacs were produced, but they were much smaller than the pollen-sacs of other stamens of the same flower at the same level (cf. I and II). At one end of the stamen there was one pollen-sac which would probably rupture on the inner side, since the parietal tissue was thinnest there. There was no indication of a second pollen-sac. The other end gave by its curved outline at any rate some suggestion that two pollen-sacs might have formed one loculus. The sac in this case would rupture on the inner side of the stamen.

Transverse sections were made of a second and somewhat older flower, and it was found that in this case there were five stamens arranged alternately with the petals, but these stamens were much less regular in shape than those in the first flower examined. The ovary in this, as in the other flowers, was normal. Sections taken at a fairly high level shewed stamens each with an irregular outline and producing pollen-sacs, but not always in the situations one would expect. Sections at a lower level shewed the appearance represented diagrammatically in VI. The stamen on the right hand was very similar to those found in the first flower and produced ovules freely from its inner surface. The typical outline, however, was less well maintained, and only one pollen-sac

was developed in each anther lobe. Of the other four stamens, two only produced ovules on the free surface. All four, however, shewed cavities radially narrow, but considerably extended tangentially. Quite normal ovules were produced on the walls of these cavities. In the case of three of these stamens one of the anther lobes appeared to be wanting; the other anther lobe formed one or two pollen-sacs. Basal sections (VII) shewed fusion of the tissues of the stamens and carpels, save in one instance where the right-hand stamen was united to a petal. Ovules were produced at this lower level, though the lower limit of the pollen-sac had been nearly reached. The small stamen on the left-hand side appeared to have become somewhat twisted, ovules coming off from its exterior surface.

In none of the other flowers examined were any further variations seen in the method of developing ovules. As no endosperm could be distinguished in any embryo-sac, whether on stamen or carpel, it could not be determined whether the ovules appearing in these strange situations had been pollinated.

A longitudinal section of another flower is diagrammatically represented at V. One massive stamen shews two fertile pollen-sacs and many ovules springing from the free inner surface of the filament from the base upwards, and the bulging mentioned above is clearly seen. The ovules arose more or less in clusters, often slightly raised on platforms or ridges on the surface of the stamen. This flower shewed stamens with cavities running through the greater part of their length, on whose walls ovules were developed. It also shewed an outgrowth from the inner surface of a petal, which on closer inspection proved to be a shortly-stalked microsporangium. The pollen-sac contained pollen-mother-cells, which, to judge by the broken-down tapetum, were fully formed. The sac was surrounded by five or six layers of cells, and in this case shewed no signs of rupture. Pollen-sacs were found in the petals of another flower of which transverse sections were made (III). One end of the petal was normal and incurved, composed of fairly regularly-arranged cells; the other end was several times as thick and was composed of cells comparable in size with those forming the main mass of a stamen. An attempt at an anther lobe was suggested by the curving outlines. A large crescentic pollen-sac was also present, whose outline followed the curve of the petal. This pollen-sac shewed distinct signs of rupture towards the inner side of the petal. Its



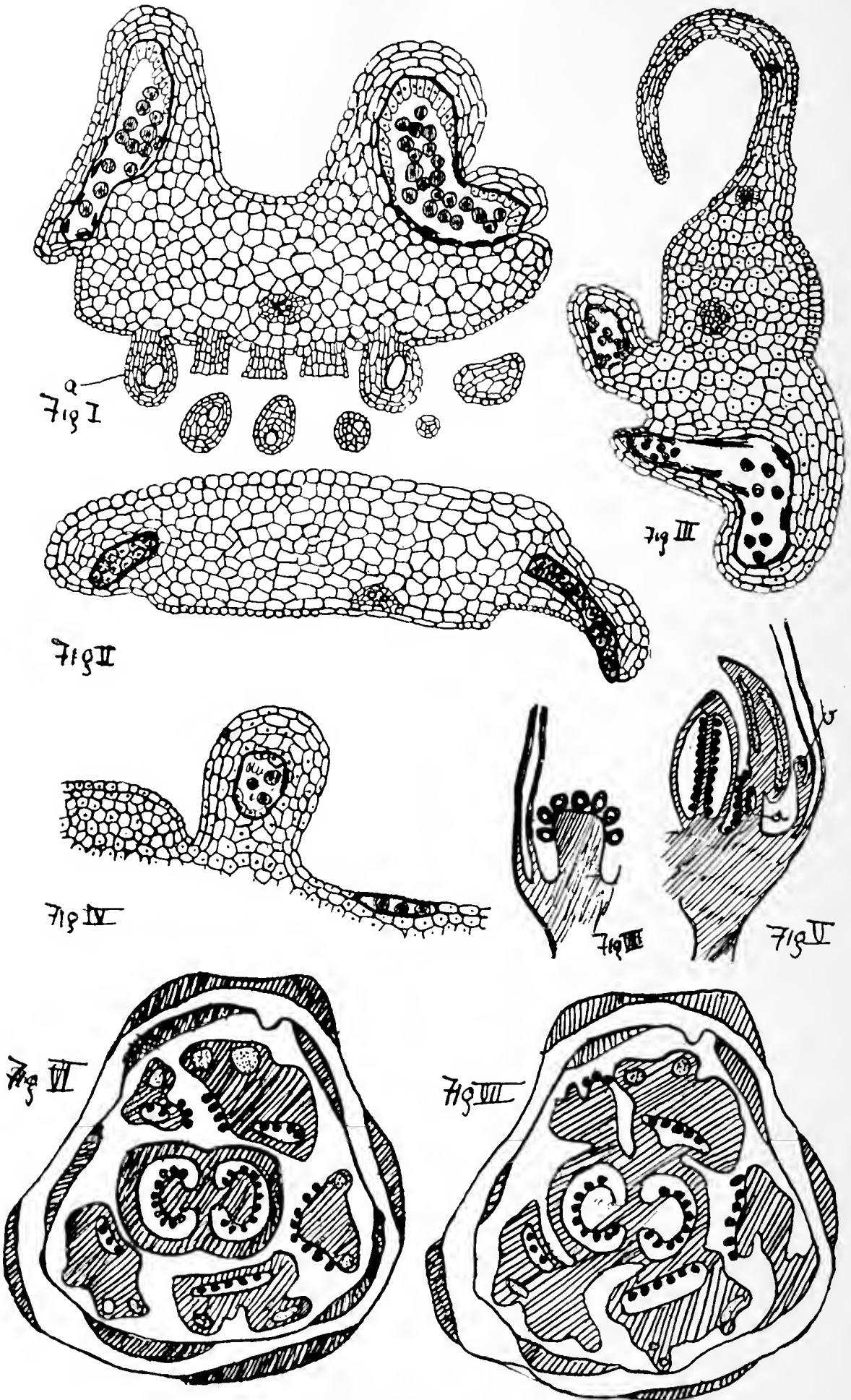


Fig. 11.



## *On Abnormal Flowers of Solanum tuberosum.* §1

tapetum had become disorganized, and the sac contained numerous well-formed pollen-mother-cells. The same petal shewed a sac in the same position as that seen in longitudinal section of the flower mentioned previously. It was deeply imbedded in tissue on all sides and showed no signs of rupture. In this case the pollen-mother-cells were either about to divide or had just divided to form tetrads.

Another flower (III) exhibited similar features. A swelling appears on the inner surface of the petal, containing a deeply imbedded pollen-sac with a few pollen-mother-cells. Some signs of a tapetum are visible, but no signs of rupture. The same section passed through the top of another pollen-sac evidently on the point of rupturing on the adaxial face.

All flowers that shewed petals developing pollen-sacs had also the full number of fertile stamens.

The material had unfortunately not been fixed for cytological examination, so that many points of interest relating to the structure of the pollen-mother-cells and the embryo-sacs of the anomalously-placed ovules, had to be left undetermined. The phenomena exhibited by these abnormal flowers appeared however to be sufficiently curious to warrant the publication of this brief note.

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### DESCRIPTION OF TEXT-FIG. II (I.—VIII.)

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- I. T.S. stamen near base. *a*, Ovules produced on the adaxial surface.
  - II. T.S. stamen, semi-petaloid.
  - III. and IV. T.S. petal shewing two pollen-sacs.
  - V. L.S. abnormal flower, shewing (*a*) ovules on a stamen and (*b*) a pollen-sac developing on a petal; diagrammatic.
  - VI. T.S. abnormal flower; diagrammatic.
  - VII. T.S. same flower near base.
  - VIII. L.S. stamen viewed from the adaxial side. The tangential section passes through the inward bulging filament and thus shews only the ovules at the apex of the ridge. The section is taken too near the axis of the flower to pass through the anther.
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ON THE TYLOSES OF *RACHIOPTERIS CORRUGATA*,

BY F. E. WEISS, D.Sc.

[WITH TEXT FIGS. 12 AND 13].

IN his description of this fern-stem, Williamson<sup>1</sup> ('77) drew attention to the presence in its tracheids of "densely packed masses of cells," which he compared with the tyloses found in the vessels of recent plants. A similar occurrence was noticed by him in a fern rachis described under the name of *Rachiopteris insignis* ('80). Recently Oliver<sup>2</sup> ('05) has found these petioles associated in such a way with the stem of *Rachiopteris corrugata* as to suggest that these two remains are the stem and leaf-stalk of the same plant. A similar section is in the collection of the Manchester Museum, being one of the specimens belonging to the late Thomas Hick. The occurrence of tyloses in both organs might be looked upon as confirmatory evidence of the connection of two fern-remains.

The identification of the remarkable "intrusive cells" with the tyloses of recent plants was again urged by Williamson<sup>3</sup> ('88) in a publication in which he discussed several cases of anomalous cell-contents in fossil plants. It was, of course, quite possible to consider these intrusive cells to be of the nature of saprophytic or parasitic fungi, as they undoubtedly are in some of the cases described by Williamson. But in the two fern-remains mentioned the general appearance of the blocked-up tracheids is so remarkably like that of vessels filled with tyloses, that one is inclined to accept Williamson's conclusions in spite of the fact that such tyloses have not been found in any living ferns according to Molisch<sup>4</sup> ('88), who made a most careful examination of about 700 plants with a view to ascertaining the distribution of these curious cells. Nor is it surprising that they should be absent from Ferns and Gymnosperms, when we consider that their main function is probably to close continuous vessels. For these latter are generally absent from the two groups of plants referred to, which, possessing tracheids, have

<sup>1</sup> Williamson, W. C. Organisation of the Fossil Plants of the Coal Measures, Part VIII., Phil. Trans., 1877. Part X., Phil. Trans., 1880.

<sup>2</sup> Oliver, F. W. Catalogue of the Collection of Sections of Fossil Plants in the Botany Department of University College, London, 1905.

<sup>3</sup> Williamson, W. C. On some anomalous cells developed within the interior of the vascular and cellular tissues of Fossil Plants of the Coal Measures, Annals of Bot., Vol. II., 1888.

<sup>4</sup> Molisch, Hans. Zur Kenntniss der Thyllen. Sitzber. d. k. Akademie d. Wiss. zu Wien., Bd. XC., VII., 1888.

less need for this form of closing a wound. Their mode of origin, too, upon which Molisch insists, as ingrowths from surrounding parenchymatous cells, seems to preclude their formation in Gymnosperms where wood parenchyma is generally absent. The fossil wood in which Sir William Thiselton Dyer<sup>1</sup> ('72) has described the existence of tyloses is, as he states, evidently that of a dicotyledonous tree, and the tyloses fill the well-defined vessels, which are, no doubt, in part surrounded by wood-parenchyma.

In many of the fern-stems and their leaf-stalks, as far as they are represented among carboniferous remains, there is apparently very little, if any, wood parenchyma present among the tracheids, and this fact renders it difficult to explain the presence of tyloses in *Rachiopteris insignis* and *R. corrugata*.

For though in the rachis figured by Williamson (Pl. 16, Fig. 20), where the tracheids are only two rows deep, it is possible for ingrowths to take place from the surrounding parenchyma on one side, yet in some cases there are three rows of tracheids of which the innermost is bounded on either side by lignified cells.

In the stem figured in his earlier paper ('77, Pl. 6, Fig. 16), the tracheids which are filled with tyloses, are seen to be surrounded on all sides with other tracheids, and no wood-parenchyma is visible. And indeed that is found to be the case regularly with large groups of tracheids in *R. corrugata*, though some, both on the inside and on the outside, abut on parenchymatous cells. One is therefore at a loss to understand how in the middle of the woody mass tyloses *can* be formed in a normal manner.

The supposition that these curious growths may after all be of a fungal nature reasserts itself, and a representation such as Williamson gives in Fig. 12 of his later paper ('88), where a hypha-like filament traverses the lumen of the tracheid to become dilated into a terminal swelling, recalls forcibly the similar dilatations of fungi formed in the tracheids of various lepidodendroid plants.

In spite of the difficulty of explaining the formation of these tyloses, I am inclined to accept Williamson's identification as correct. The occurrence of filamentous outgrowths terminating in dilated tyloses may be a necessity where, as in the case of the rachis, parenchymatous cells are found only on one side of the tracheids. In this case it may be necessary to close the distal portion of the lumen by tyloses growing at first as elongate filaments between the nearer protrusions until they reach the further side of the cell-space, where they dilate into normal tyloses.

<sup>1</sup> W. T. Thiselton Dyer. On some Fossil wood from the Lower Eocene. Geol. Magazine, Vol. XCVI., 1872.

How the tyloses are formed when the tracheid is surrounded on all sides by other tracheids, as in Fig. 12 of this paper, is more difficult to imagine. It is, of course, conceivable that a tylose might push onwards from tracheid to tracheid, constricting when it came to a pit membrane, but I hardly think that can be their course of development. In a very thin section of *Rachiopteris insignis* in the Manchester Collection there occur in the angles where three tracheids meet small spaces which may have been occupied by a minute parenchymatous cell, like the small cells met with in a similar position in *Sphenophyllum*. From the absence of walls, however, *Rachiopteris* could only have possessed one such cell, the walls of which must have been adjacent to those of the tracheid. Occasionally one finds the two adjacent walls of two tracheids split apart, and it is quite conceivable that in some cases, at all events, there may have been narrow parenchymatous cells between two

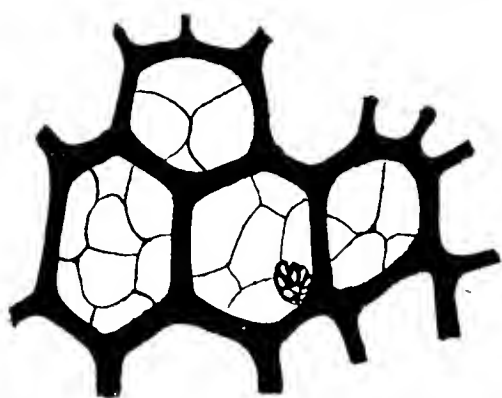


Fig. 12.

Fig. 12. Portion of the lignified tissue of *Rachiopteris corrugata* (R447) shewing ordinary tyloses and an anomalous type.



Fig. 13.

Fig. 13. Anomalous tylose in angle of tracheid enlarged to show pitted wall.

tracheids, which may have been rendered unrecognisable by compression previous to, or since, fossilisation. In one instance, at all events, I have met with an appearance which might be explained by the existence of such delicate parenchymatous cells between what appeared to be adjoining tracheids. The general aspect of this preparation, however, suggests that these appearances may be due to decay having set in before the stem became fossilized, and the separation of the tracheids may be due to partial decomposition.

A strong argument in favour of the view that these intrusions are really of the nature of tyloses is the occurrence in one of the sections in the Manchester Museum (R 447) of an intracellular projection of somewhat unusual appearance, and closely resembling some peculiar tyloses which Miss Rose Jordan described some two-

and-a-half years ago in this Journal.<sup>1</sup> As will be seen from the accompanying sketches (Figs. 12 and 13), in this particular instance the cellular protrusion differs from the ordinary tyloses in having its walls thickened (probably lignified), and the thickening has taken place in such a manner as to give the structure the appearance of a small pitted tracheid. As the pits are of irregular shape and somewhat pointed, the marking at first sight looks slightly spiral. This is exactly the appearance of those described by Miss Jordan, and there is thus a very close agreement between this thickened tylose of *Rachiopteris corrugata* and those from a section of *Cucumis* figured in Plate X. of Vol. II. of the NEW PHYTOLOGIST. These latter are undoubted tyloses, as their protoplasmic contents and nuclei were often visible. It was noticeable in the case of these latter that they only occurred in vessels which were not yet blocked by ordinary tyloses, while as the one figured in this note shows, the peculiar tylose in *Rachiopteris* occurs in a vessel in which the lumen is occluded by thin-walled cellular tissue, as it is in the adjoining vessels. It is, of course, possible that it may have been formed earlier than the thin-walled tyloses, and indeed its more or less spherical shape suggests that it had become thickened before it had met the outgrowths from the other sides of the vessel. In *Cucumis*, too, it is quite conceivable that vessels in which the lignified tyloses were formed might subsequently become closed by the ordinary form of outgrowths, for numerous young thin-walled tyloses were met with and are figured by Miss Jordan among the thickened ones. There seems therefore in this particular to be no real difference between the anomalous tyloses met with in two such widely different plants as a fern of the Coal Measures and a dicotyledon of to-day. The occurrence of this anomalous tylose of course greatly strengthens the probability of the thin-wall protrusions being also of the nature of tyloses. At the same time we still remain unable to explain satisfactorily the mode of origin of these intrusive cells, for the anomalous tylose also arises in a tracheid apparently surrounded on all sides by lignified cells. It will, however, be seen that it, like most of the thin-walled protrusions, arises near the angle formed by adjoining tracheids, and thus points to the possibility of the existence of hidden parenchymatous cells in these angles.

In conclusion I should like to mention that we have in the collection of the Manchester Museum a section of *Zygopteris Grayii* (R443) which has a few tyloses both in tracheids of the stem and also in one of the leaf-trace bundles.

<sup>1</sup> Jordan, Rose. On some peculiar tyloses in *Cucumis sativus*, NEW PHYTOLOGIST, Vol. II., No. 9, November, 1903.

## CURRENT INVESTIGATIONS IN ECONOMIC BOTANY.

*(Continued from Vol. IV., page 114.)*

BY WILLIAM G. FREEMAN.

## SEMINAL SELECTION OF SUGAR CANES.

In the previous articles we have devoted some attention to bud-variations or sports and chemical selection of the sugar-cane and indicated broadly the results of the efforts made to produce races of canes of higher sucrose yield by taking advantage of variations, in the one case correlated with differences in external characteristics of the plants and in other to be recognized only as the result of chemical analysis of their juice. We now turn to the third method which is employed in practice, namely, seminal selection.

The prosecution of work along this line possesses especial interest in the case of the sugar-cane owing to the fact that it was for long generally supposed that the sugar-cane did not produce seed. Thus Darwin in his "Variation of Animals and Plants under Domestication," remarks that the sugar-cane "which grows vigorously and produces a large supply of succulent stems, never, according to various observers bears seed in the West Indies, Malaga, India, Cochin China, or the Malay Peninsula." This view was held until as recently as 1887 in which year Soltwedel in Java proved that the plant did at times produce fertile seed. In the following year Harrison and Bovell in Barbados reported the discovery of sugar-cane seedlings found growing spontaneously in the fields, an observation which they confirmed in the following year by actually raising young plants from seeds. There are some grounds for supposing that sugar-cane seedlings were raised in Barbados about 1860 but it was not until 1887-8 that the independent discoveries in Java and Barbados definitely established the fact that the sugar-cane does at times bear fertile seed. The practical value of the discovery was at once recognized and an enormous amount of care and labour has been and is being devoted in many parts of the world to the raising of improved races of seedling canes. Progress has been slow owing to (1) the flowers of the plant being so small that controlled hybridization is very difficult, and (2) the long period which intervenes between the first raising of a seedling and the pronouncement of the verdict as to whether the resultant plant is good or not.

To deal with the latter difficulties first, let us summarize the

cultural procedure in the West Indies. The parent canes flower or "arrow" in the dry season (about November) of one year. The small seeds are sown in boxes covered with glass, and the young seedlings after being pricked out into pots are ready for transplantation into the open ground in the following April or May.

During the first year of their life growth is comparatively small and at the end of this period all that is possible is to select the more vigorous seedlings for further propagation in the ordinary way by cuttings. At the end of the second year a small number of plants will be available grown from each of the original seedlings and those showing desirable cultural characteristics are selected, some of their canes crushed and their juice analysed. The best are again propagated by cuttings and the plants selected by cultural and chemical characters. The process is repeated and it usually requires about six years before enough plants are available to allow of plots of say 100 plants each, all derived from one original seedling, being grown on several different estates, or of one plot of perhaps ten acres being grown as an industrial experiment on a single estate. When it is remembered that in addition to the percentage of sucrose and glucose in the juice the value of a sugar cane depends on its ratooning properties (*i.e.* of developing successive annual crops from the same rootstock after the previous growth of stems have been cut) on its resistance to disease, on its milling characters, on the value of the crushed cane as fuel and numerous other characters, and that accurate knowledge on these points demands trial of each variety on an estate scale with plots of several acres in extent and for several years, it must be conceded that the practical difficulties confronting those engaged in the work are sufficiently serious to prevent rapid progress.

In practice it is necessary to carry on the early selections in small plot experiments, rigorously rejecting each year all but the very best canes and finally testing the few survivors on a larger scale before recommending them to planters for trial on a sufficiently large scale to allow of an authoritative opinion being expressed. The following example from British Guiana will serve to illustrate the scale on which seedlings have been raised and the comparatively small number which have passed through the selection ordeal. During the years 1896 to 1901 some 314,000 seedlings were raised, of which 75,000 were transplanted into baskets and some 19,000 cultivated in the fields, but the net result was that only 21 were finally recommended to planters for estate trial and of perhaps not more than three have stood the test of several seasons' trial and

are now cultivated on an extensive scale not only in the West Indies but in other parts of the world.

The other difficulty has been due to the small size of the flowers combined with the general habit of the plant. The inflorescence of the sugar-cane consists of a feathery plume not unlike that of the more familiar Pampas-grass, borne some 12 or 15 feet above the ground, and consequently rigidly controlled hybridization as practised on flowers of large size and readily accessible appeared almost impossible. At first no selection was made at all, but any seeds whatever their parentage were taken and plants raised in the hope that some might prove to be of value. An advance upon this method was to select certain canes as parents and to collect seed from these only, but in these cases although the female parent was known the parentage on the male side was unknown and the result found in various parts of the world was that the majority of the seedlings were inferior to the plants from which they were produced.

To ensure the best results it is essential that it should be possible to select both parents and various methods have been suggested and tried to ensure the crossing of chosen varieties. Adjacent plots, or alternate rows in one plot, of two selected varieties known to flower at the same time were arranged but although some of the seeds produced were doubtless the result of cross pollination too much was left to chance to ensure very satisfactory results.

Another method, easy to carry out, was to 'bag' the inflorescences of the selected mother canes and when the pistils were ripe to shake into the temporarily opened bags pollen from the inflorescence of the other selected variety. By this means some, but not necessarily all the seeds would probably be the result of cross pollination between the two varieties.

In 1894 Wakker discovered in Java that the Cheribon cane had practically unisexual flowers the pollen not being fertile, and Kobus planted plots with alternate rows of this Cheribon cane and of an Indian cane, Chunnee, with normal flowers. With proper precautions the fertile seeds must have been the result of the pollination of the Cheribon by the Chunnee, and several thousand hybrid canes were raised.

In 1904 in Barbados Lewton Brain succeeded, under considerable practical difficulties, in actually emasculating and bagging inflorescences of one variety and definitely pollinating the flowers later with pollen from another variety. A few seedlings were raised



of known parentage on both sides but details are not yet available as to their characteristics. The experiment is of great interest and importance as demonstrating that rigidly controlled hybridization of the sugar cane is practicable and steps are being taken by others to continue the work along these lines.

Having now sketched the methods employed in the raising of seedling canes and the principal practical difficulties which have to be contended against it is desirable to review briefly the main results attained, and to do this it is desirable to look back a few years and note what were the conditions which gave an impetus to the raising of seedling canes. About twelve years ago the "Bourbon" was the standard cane of the West Indies and was very extensively cultivated, but it became very subject to the attacks of fungoid diseases, so much so that in some cases in bad seasons whole fields were rendered practically worthless. Effort was made to combat the disease and attention was early directed to the question of finding disease resistant varieties. In Barbados for instance in 1891 the variety known as Caledonian Queen gave good results on an estate where it had been planted along with the Bourbon although the latter canes were so attacked that they had to be destroyed. Seedling canes were also tried and at the experiment station at Barbados the seedling B. 147 gave during the years 1894 to 1898 an average of nearly 2,000 lb. of sugar per acre over the yield of the Bourbon under similar conditions, the actual figures being B. 147, 7,190 lb., Bourbon, 5,210 lb. Another seedling cane B. 208 has also proved itself of great value and these two varieties are now cultivated in the colony on an extensive scale, although the most widely grown cane at present is White Transparent one of the so-called "older varieties" of unknown origin. The Bourbon cane in Barbados has almost entirely disappeared. The two Barbados seedlings have not only given good results in the country of their origin; B. 208 is according to Dr. Cousins "well suited to all parts of Jamaica and is probably the best cane now available." It has also given good results and proved of considerable economic value in Antigua, St. Kitt's and Nevis, in British Guiana, and as far afield as Louisiana and Queensland. Seedlings of high value have also been raised in British Guiana (these are designated by the letter D) and again quoting Dr. Cousins "D. 95 has [in Jamaica] proved a great success. This cane has give double the yield of crystallized sugar per acre, as compared with the Jamaica cane and upon a commercial scale."

Much more evidence might be called, but the above will probably be sufficient to prove that seedling canes have proved to be a factor of great economic importance in raising the sugar industry of the West Indies from the depressed condition into which it had fallen, due in considerable measure to the prevalence of fungoid disease which attacked the old standard varieties from about 1894 onwards.

The great expectations once held of seedling canes may not have been realized, and the evidence available indicates that perhaps about 25 per cent. is the maximum amount of sugar which sugar-canes will yield and be profitable. Increase of yield beyond this point must be sought rather by increasing the tonnage of the canes than by attempting to enhance their sucrose contents.

Disease resistance may be only relative. It must be remembered that in the case of the older canes propagation by cuttings from canes permeated with fungal hyphae ensured the continuance of the disease as each cutting carried the disease within it and had not to wait for infection. With seedlings a new race was started free at first from disease but as this stock, like the former, is propagated year after year by cuttings the diseases will probably be propagated too, so that in the course of a few years another new race would be required to ensure a relatively disease free stock.

The greatest hope for the future lies in the expectation that it may become increasingly practicable to raise canes of definitely known parentage from carefully selected plants possessing to the greatest degree the characteristics of disease resistance, high sucrose yield, heavy tonnage of cane and the other properties which have been previously mentioned as marking a sugar-cane of high economic value.

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NOTES FROM THE CAMBRIDGE BOTANY SCHOOL.

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In the first number of the NEW PHYTOLOGIST<sup>1</sup> a short account was given of the method adopted in the practical work connected with advanced courses of lectures on Pteridophytes, Gymnosperms and Plant-Anatomy in the Cambridge Laboratory. We occasionally notice morphological features in plants under examination which do not appear to have been previously recorded, and it occurred to me to ask the Editor of this Journal to allow us to send brief notes on such points as seem to us of sufficient interest to publish.

A. C. SEWARD.

<sup>1</sup> Vol. I., No. 1, 1902, p. 14.

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I.—ON A SUGGESTION OF HETEROSPORY IN

*SPHENOPHYLLUM DAWSONI.*

By D. THODAY, B.A.

(Scholar of Trinity College, Cambridge).

[WITH TEXT-FIG. 14.]

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It is generally agreed that heterospory has arisen independently in several different groups of Vascular Cryptogams. In some of these groups the differentiation has proceeded much further than in others; in some its beginnings are suggested. Among fossil plants *Calamostachys* is interesting in this connexion, since one species, *C. Casheana*, is distinctly heterosporous, although the megaspores are only three times as large as the microspores; while *C. Binneyana* is isosporous; but abortive spores have been figured by Williamson and Scott,<sup>1</sup> the survivors attaining a size slightly above the normal. Abortive spores are found also in the megasporangia of *C. Casheana*.

Up to the present nothing of this kind has been recorded for *Sphenophyllum*. Renault's opinion that one of his French specimens showed heterospory is considered by Zeiller<sup>2</sup> and by Williamson and Scott to be based on a misinterpretation, and it is now generally agreed that *Sphenophyllum* is homosporous. As will be seen from the figure, the present observation shows that something of the

<sup>1</sup> Williamson and Scott, Phil. Trans. R. Soc., Vol. 185B, 1894, p. 911.

Zeiller, Mém. Soc. Géol. France, 1893.

kind described for *Calamostachys* may have been going on in *Sphenophyllum Dawsoni*.

The large size of the spores figured and the abortive spores accompanying them were noticed during the examination of a section in the Cambridge Botany School Collection. The slide in question was prepared by Mr. Lomax from a specimen obtained from Shore, Littleborough, Lancashire; it is an oblique tangential section of a strobilus of *Sphenophyllum Dawsoni*, which, judging from this and another more median section of the same specimen, was 15 mm. long by 8 mm. in diameter. The number of internodes preserved appears to be six, and this conclusion is supported by a comparison of the total length with the distance between two successive whorls (about 2.5 mm.); but towards the apex, which is represented in the more median section, there is some indefiniteness.

In the lowest whorl but one in the section first mentioned a sporangium occurs (see Fig. 14) which contains fewer and larger spores (*a. a.*) than the adjacent sporangium, together with a number of abortive spores (*b. b.*) From a number of measurements of the diameters of the spores, the average in the sporangium in question is  $106\mu$ ; the maximum diameter is  $120\mu$ , and several reach  $115\mu$ . Similar measurements in the adjacent sporangium figured give an average of  $83\mu$ , with a maximum of  $90\mu$ . The presence of the characteristic spines (*c. c.*) shows that the spores in both sporangia had reached maturity.

The maximum diameter recorded by Williamson and Scott for spores of *S. Dawsoni* is  $104\mu$ .<sup>1</sup>

<sup>1</sup> Loc. cit., p. 939.

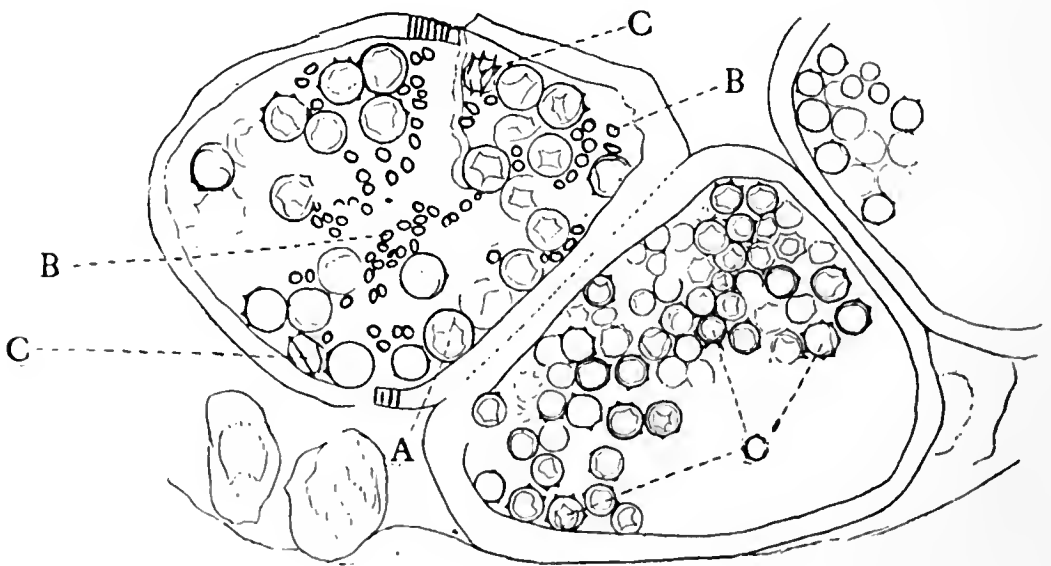


Fig. 14.

In the other more median section the lowest whorl is represented by fragments of two sporangia, and in one of these a few large spores are accompanied on one side by a large number of abortive spores. These large spores, like the sporangium containing them, have not been well-preserved, but the only one of them which allows of satisfactory measurement has a diameter of about  $135\mu$ . Of the other sporangia, most have spores of the normal dimensions, but in one or two a few abortive spores occur, and the survivors are larger than the normal.

It is interesting to note that the sporangia containing the larger spores occur at, or near, the base of the strobilus, just as is the case where advanced heterospory is found.

In comparison with *Calamostachys*, abortion has proceeded a step further than in *C. Binneyana*, but not so far as in *C. Casheana*. If one imagines the spores produced in tetrads, not merely some of the spores in the tetrad, but whole tetrads, have aborted, with a corresponding increase in the size of the survivors, in the extreme case to about one-and-a-half times the normal diameter.

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## SKETCHES OF VEGETATION AT HOME AND ABROAD.

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### II.—SOME ASPECTS OF THE VEGETATION OF SOUTH AFRICA.

By F. E. WEISS, D.Sc.

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### PART III.—RHODESIA AND THE VICTORIA FALLS.

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THE passage through Bechuanaland and the visit to Rhodesia coincided, as our stay in the Transvaal had done, with the dry season, so that the country had a very arid and parched appearance. The land traversed during the first part of the journey through Khama's country was flat and practically a grass steppe, though northwards trees became more numerous and the aspect more like that of a savannah, in parts quite park-like. The trees were largely Leguminosæ, many of them being acacias, some of which were just coming out into flower, often on quite leafless branches.

The Matoppos, which lie a little south of Bulawayo and which we visited from that town, are a series of rock Koppjes, showing a most curious weathering of the granite rocks into enormous rounded boulders on the tops of the small hills. On the slopes of the latter the vegetation was more stunted and xerophytic in aspect. Numerous bushes of the drought-resisting *Myrothamnus*, mentioned in the description of the Transvaal, were found on the broken ground, and here and there tree-euphorbias such as were met with on the higher ground of the bush-veldt. Near the foot of the hills one of the most characteristic trees was the *Afzelia*, the large woody pods of which contain seeds provided with a scarlet or orange aril, and sold as curiosities.

North of Bulawayo the more abundant annual rainfall is clearly noticeable, even in the dry season, by the more considerable number of trees and their greater size. The savannah now gives way to a more continuous, though not very close, woodland. Such was the so-called "Teak forest," of which most of the trees seemed to be members of the Leguminosæ. Most conspicuous were Bauhinias with light-grey somewhat mottled stems, their characteristic bilobed leaves remaining dry and brown on the branches and presenting the aspect at a distance of a beech tree in the late Autumn. Besides these we noticed a *Pterocarpus echinatus*, its large rounded pod provided with winged margin and very spiny centre. Other trees, too, could be recognised by their pinnate leaves and leguminous fruits as belonging to the same natural order. At this time of the year there was very little undergrowth except the dried remains of grasses and other herbaceous plants. Here and there a *Helichrysum* or a drought-resisting member of the Thymelæaceæ might be seen. In passing through this district we encountered an enormous swarm of locusts flying south and darkening the sky as they approached. It gave one a vivid idea of the havoc they could make in any region where irrigation would supply them with the necessary food, and indeed in the Northern Transvaal we had already seen them, though in lesser numbers, on cultivated land.

With slight variations in the density of the woodland, the same vegetation continued up to the Zambesi, most of the trees showing by deciduous foliage their adaptation to a prolonged period of drought. Among these latter trees one of the most remarkable, by the swollen and elephantine appearance of its stem, was the Baobab (*Adansonia*), which became more frequent as we approached the

Victoria Falls. In the dry forest we picked up numerous fruits of *Harpagophyton* with their sharp recurved spines. The herbaceous upper part of the plant had died down, but the tuberous root no doubt persisted underground. On the rocky faces of the winding river, below the falls, the highly xerophytic *Selaginella imbricata* was very common, its frond-like branches tightly coiled up in crosier-like manner awaiting the summer rains. A few Liliaceæ with hard resistant foliage like Aloes and Sansevierias told of the extreme drought for which the vegetation had for the most part prepared. But near the river the trees and shrubs were less strongly xerophytic and no doubt owed their existence in part to the moisture which the atmosphere must get even at a distance from the Mosi-ou-tunya, or the "Smoke that sounds," as the natives call the Victoria Falls. For the cloud of spray ascends a hundred feet above the top of the Falls and must exert some considerable effect on the humidity of the atmosphere. The deeper layers of the soil too, at some distance from the river banks, must have a sufficient store of water even in the dry season to supply abundant moisture to deep-rooted plants such as trees, even though the herbaceous plants may have died down. Thus one found on the banks such large trees as *Rigelia pinnata* in full foliage and with large pendant racemes of brown flowers that are visited by sun birds. Palms, too, such as *Phœnix reclinata* and *Hyphaene*, are seen on either side of the river and particularly in the sheltered kloofs where, with the tangle of lianes and ferns, they present quite a tropical aspect. Of the shrubs near the Zambesi a large *Ipomœa* was the most conspicuous, its leafless branches being covered with large pink flowers, while in the slow flowing water above the falls grew tall Papyrus plants and the aquatic *Jussieuia*.

In great contrast to the absence of herbaceous plants in flower in the dry forests during the prevailing drought, was the abundance of small plants in active vegetation and in flower on the small rocky islands which break the long line of the Falls. Here, surrounding the trees in the centre of the island, is a well-watered and in some parts even boggy expanse covered with grass and numerous small herbaceous plants.

Most conspicuous by its large mauve coloured flowers on a slender inflorescence was *Rhamphicarpa tubulosa* (Scrophulariaceæ), while in the moister parts small yellow and purple Bladderworts (*Utricularia*) and a short Pipewort (*Eriocaulon*) were very common. Those unfamiliar with tropical vegetation were

perhaps most interested in the Podostemaceæ found on the rocks or in the shallow water above the Falls. One of these was of small feathery growth, red in colour and resembling a seaweed, but absence of flower or fruit made it impossible of identification. The other, which grew in large tufts on the now exposed rocks, was dried by the sun and studded with fruits like the capsules of a moss. It looked very unlike a flowering plant. It seems to be a species of *Dicraea*.

The so-called Rain Forest on the opposite side of the gorge into which the Zambesi precipitates its waters, is in marked contrast to the rest of the vegetation of the district. A dense screen of evergreen *Eugenias* breaks the force of the spray which dashes up against it, and behind this living screen we have a magnificent development of vegetation favoured by the abundant and almost permanent moisture supplied by the falling spray. Tall luxuriantly growing trees, mostly evergreen, covered with epiphytes and festooned with lianes, make it almost impossible to believe that one is really in a region with a pronounced dry season.

Of the trees one of the tallest and most abundant was a *Mimusops* (Sapotaceæ), the olive-like fruits of which are edible, while the wood is of considerable value. Most interesting, too, was a large *Ficus*, which produced its numerous inflorescences close to the base of the stem, like the Indo-Malayan *Ficus rhizocarpa*. In the more open parts of the forest away from the Falls, where the atmosphere was drier, *Phoenix reclinata* became more abundant, though numerous young palms are found inside the forest. Here, however, the undergrowth is made up very largely of ferns, of which the silver fern *Cheilanthes farinosa* was the most conspicuous. A *Psilotum*, too, was seen on a dead tree trunk, otherwise clothed with Mosses. Mosses, indeed, were numerically very abundant, but not very varied in kind. Facing the Falls and outside the Rain Forest the rocks were covered with a brownish gelatinous growth which seemed to consist largely of globular masses of Cyanophyceæ. The view from these slippery rocks of the long line of Falls, broken by little rocky islands, the ceaseless play of the falling waters accompanied by the resounding noise of the torrents dashing themselves against the bottom of the gorge, four hundred feet below, all this in the setting of a semi-tropical vegetation, will remain as an indelible picture in the memory of all those who were privileged to accompany the British Association on its visit to South Africa.

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THE ABSENCE OF AN EPIDERMIS IN THE ROOTS  
OF MONOCOTYLEDONS.

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A SUGGESTION.

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IT is a well known fact that the iodine test for starch always fails in the case of the leaves of certain plants, especially many Monocotyledons, since in such leaves sugar only is present. Stahl<sup>1</sup> has shewn that the presence or absence of starch is a symptom of a strong or weak transpiration current, and he accordingly divides plants in two classes:—I. Starch-leaved, strong transpirers, II. Sugar-leaved, weak transpirers. He has pointed out that there is great competition amongst plants for the salts in the soil, and that fungi are especially successful in this struggle, as is shewn by the fact that their ash is extraordinarily rich in mineral matter. There are two ways in which a normal green plant may attain success in the struggle for salts. One way is to have a very strong transpiration current, so as to secure a great “turn over” of water. This is the method adopted by the starch-leaved plant. The other method adopted by the sugar-leaved plant is to live symbiotically with a fungus, and to profit by its power of securing salts. This plan seems to be more general than is commonly supposed. According to Stahl about one half of the vegetable kingdom is mycotrophic! Stahl finds that a large proportion of the Monocotyledons characteristically belong to the sugar-leaved mycotrophic class, especially the Liliifloræ. The Gramineæ on the other hand are starch-leaved and autotrophic. That the aid of a mycorrhiza would be particularly valuable to a Monocotyledon becomes clear when we recall the usual life history of a member of this class. Miss Sargent<sup>1</sup> has brought forward a large body of facts on which she bases the theory that the Liliifloræ are the most primitive of the Monocotyledons, and have been evolved from the Dicotyledons through the adoption of the “geophytic” mode of life, which is adapted to a climate in which a long dry season is succeeded by a short rainy season. A “geophyte” remains buried beneath the soil as a tuber, bulb, or root-stock for the greater part of the year, and only puts out roots and leaves during its comparatively short growing season. Now a geophyte which has to produce a fresh

<sup>1</sup> Pringsheim's Jahrbuch, 1900.

<sup>2</sup> Annals of Botany, January, 1903.

root-system every growing season, and which needs to get its life processes into full swing at the shortest possible notice, cannot possibly tap so large an area for salts as an ordinary herbaceous plant with a perennial root-system. Also even if it tapped an equal area it would need to take in salts much more quickly to make up for the shortness of its growth-period. This seems to indicate that the aid of a mycorrhiza would be particularly valuable, as a more effective and much less costly method of obtaining salts, than the production of a very elaborate root-system. Dicotyledons have a root-epidermis (climacorrhizic, type of Van Tieghem) while Monocotyledons are characterised by the *absence* of such an epidermis (liorhizic type). The point upon which I wish to lay stress is that the absence of epidermis in the roots may conceivably facilitate the entrance of the fungus, and this character (though it may have arisen independently, and have been simply utilised in this connexion) might possibly have been evolved in connexion with the mycotrophic habit of life. Its retention in such specialised Monocotyledons as the Gramineæ, which have become strong transpirers and have given up the mycorrhiza, would then be explained merely as a hereditary trait which has survived, although its original purpose is lost.

A. R.

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## THE VEGETATION OF THE SCOTTISH HIGHLANDS<sup>1</sup>.

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WE know of no more interesting and attractive general account of the vegetation of a country than the present work by Mr. Hardy of University College, Dundee. As its title implies it is no more than a sketch of the leading features of the vegetation. The writer passes quite lightly over the different plant-formations met with, some of which have already been closely studied by R. and W. G. Smith, but his broad general standpoint, and the different points of view from which he surveys the vegetation, furnish the reader with a most illuminating *coup d'œil*.

<sup>1</sup> Esquisse de la géographie et de la végétation des Highlands d'Ecosse, par Marcel Hardy. Paris, 1905.

In a general chapter on the physical geography, the climate and the geology of Scotland, Mr. Hardy shews that the Highlands fall naturally into an Eastern and a Western "Domain." The difference in character of these is determined partly by the geology, but mainly by the climate (especially rainfall), and though the floristic composition of the flora is very uniform over the whole region, the preponderance of the various plant-formations is markedly different in the east and west. After discussing their physical characteristics Mr. Hardy takes a rapid survey of the remains of primitive forest of the two domains, and concludes that two altitudinal zones—an oak zone and a pine zone—can be distinguished in each case, though the latter was probably much better developed in the east than in the west. The "districts" of the highlands—four in the western and five in the eastern domain—are then briefly characterised, and their often striking peculiarities brought out.

The second part of the work is devoted to a consideration of the actual plant-associations now met with, under the headings of forests, grasslands ("prairies") and moors ("landes.") One of the chief points brought out is the dominance of grassland in the west, and of moorland (particularly heathland) in the east, corresponding with the lower rainfall and partly with the more porous rocks of the Grampian *massif*. The peat-problem is discussed, but the author does not consider that we know enough, in spite of the enormous literature of the subject, to arrive at any very definite conclusions as to the historical evolution of the great peat-masses. An important feature of the discussion of the plant-associations is the prominence given to the important questions of the succession of associations and of their evolution one from another. Many interesting series are given, actually observed by the author, or inferred from various evidence.

A most interesting part of the work is that devoted to the "topographical units," four of which are distinguished, the "carse" or low-lying alluvial lands around the great estuaries, the "straths" or broad lowland valleys, the "glens," or valleys in which erosion is still going on, and the mountains, each characterised by its own physical features, scenery, soil and vegetation.

In the concluding part the relation of vegetation to man is dealt with, in a most attractive, though necessarily cursory manner. This section of the work shews very clearly the influence of Geddes, to whose inspiring influence the author, in common with many

other young Scottish workers, owes much. The contrasts between the Highlands and the Lowlands, between the East and the West, are first touched upon. The effect of geographical situation, and of topographical character, of climate, and of vegetation upon the inhabitants, and the reactions of the human population and its history upon the vegetation, are briefly surveyed. The social and economic differences of the altitudinal zones—the maritime zone, the zone of the carse, the agricultural zone, the pastoral zone, the forest zone (very reduced), and the alpine zone—are described, and the leading plant-associations in their relation to man are also shortly dealt with. A final page summarises the probable evolution of the plant-covering since the glacial epoch, a somewhat melancholy history in its later phases, when “le roi du dollar et du stock-exchange, dernier avatar du chasseur à la hache de pierre, reprend possession des pentes dénudées, tandis que le pays se transforme en un désert artificiel.”

The future, it is to be hoped, may be brighter. Mr. Hardy shews good reason for believing that the deer forests and grouse moors of the east may be re-afforested with comparative ease, the lower levels with deciduous woods and the higher with larch and pine, while the west will probably always remain predominantly pastoral, though much may be done to improve the pastures, and extensive planting of spruce may arrest the present excessive denudation.

The work is illustrated by a few (rather poor) half-tones, and numerous outline maps and diagrammatic sections. A general vegetation map is referred to, but does not accompany the work in its present form. Mr. Hardy is to be warmly congratulated on his broadly conceived and fascinating sketch, his skill in bringing together the data which furnish the basis of his outline and in indicating the problems most worthy of further study.

A. G. T.





Fig. 1.

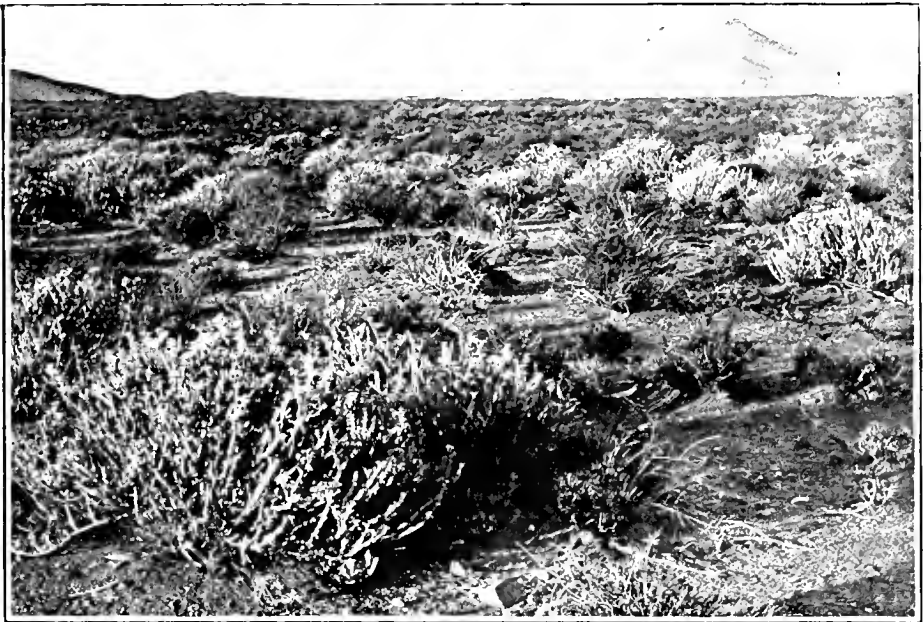


Fig. 2.

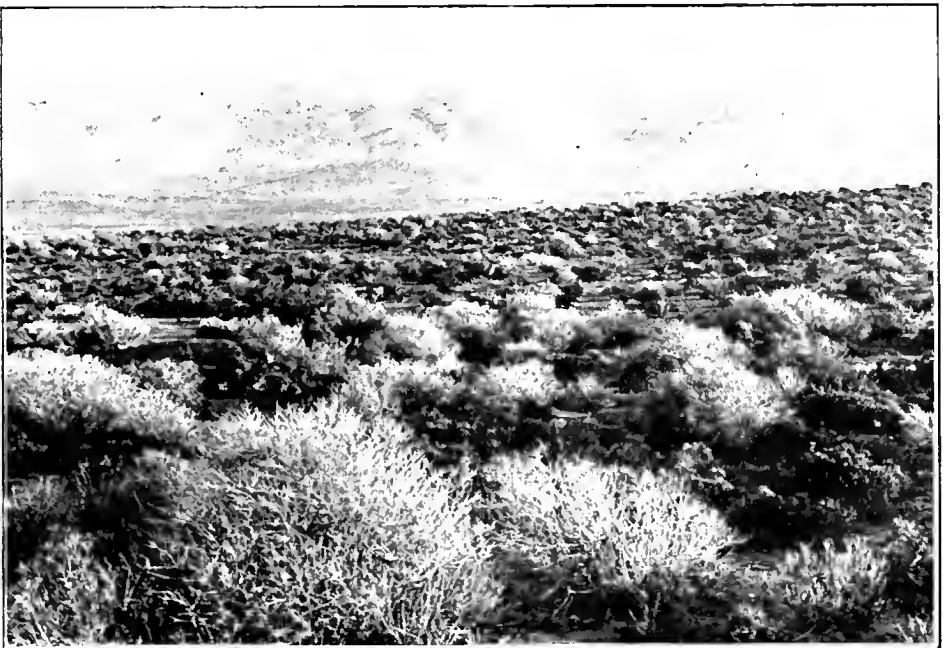


Fig. 3.

*R. H. Yapp, photo.*





Fig. 1.

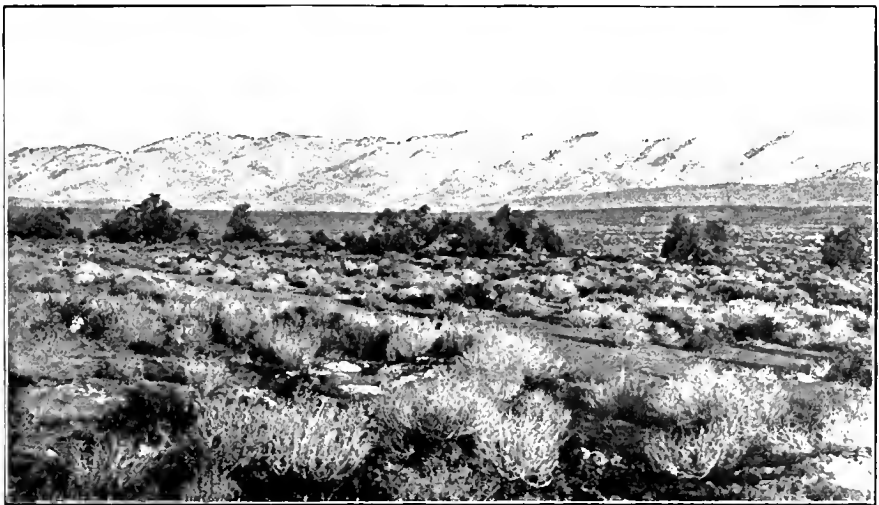


Fig. 2.

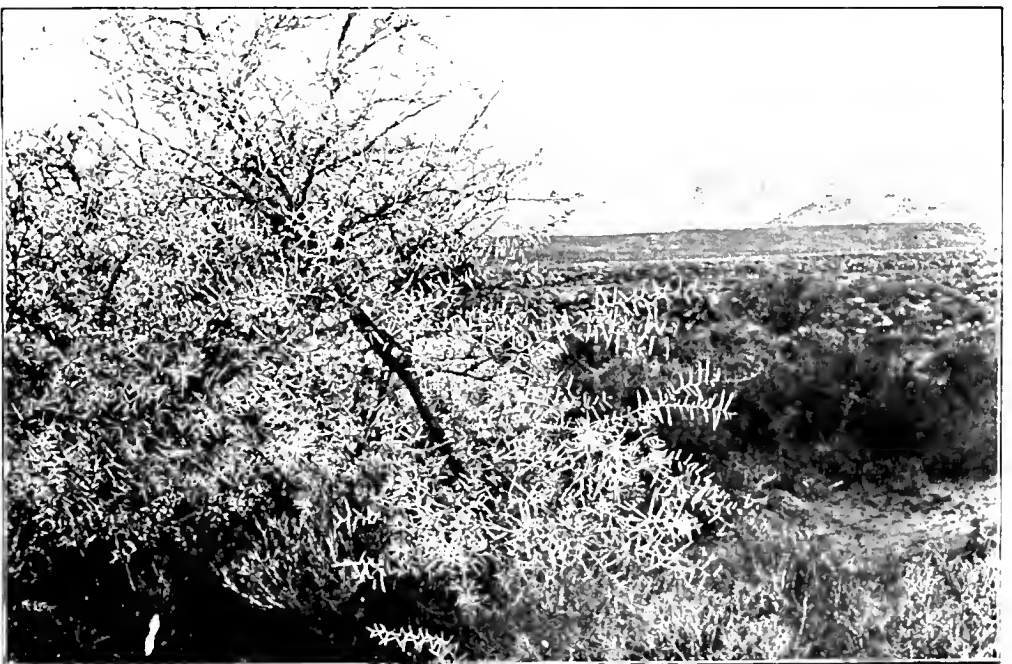


Fig. 3.

*F. E. Weiss et R. H. Yapp, photo.*





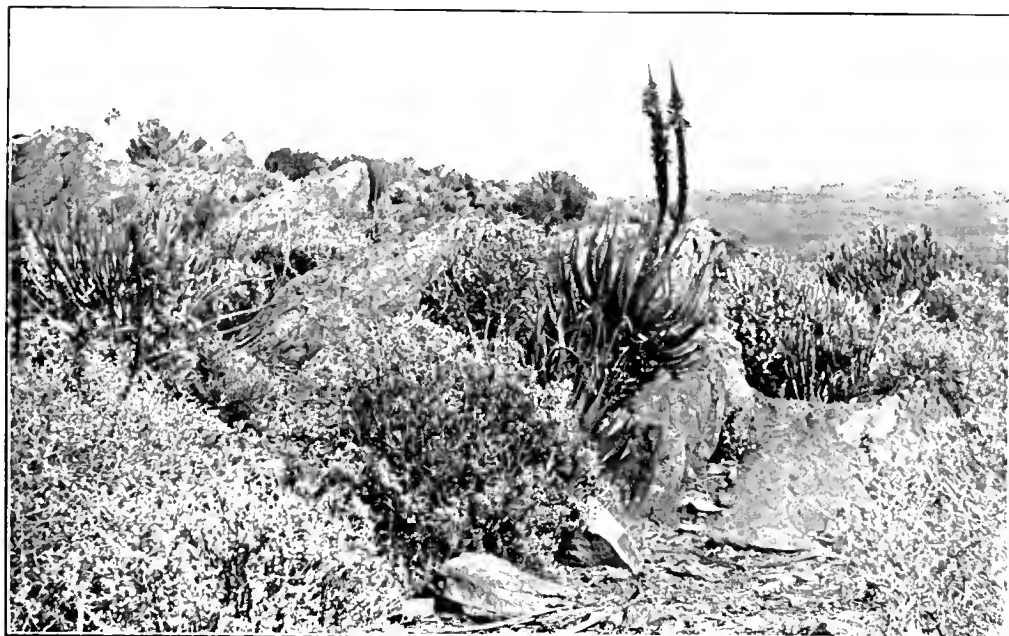


Fig. 1.



Fig. 2.



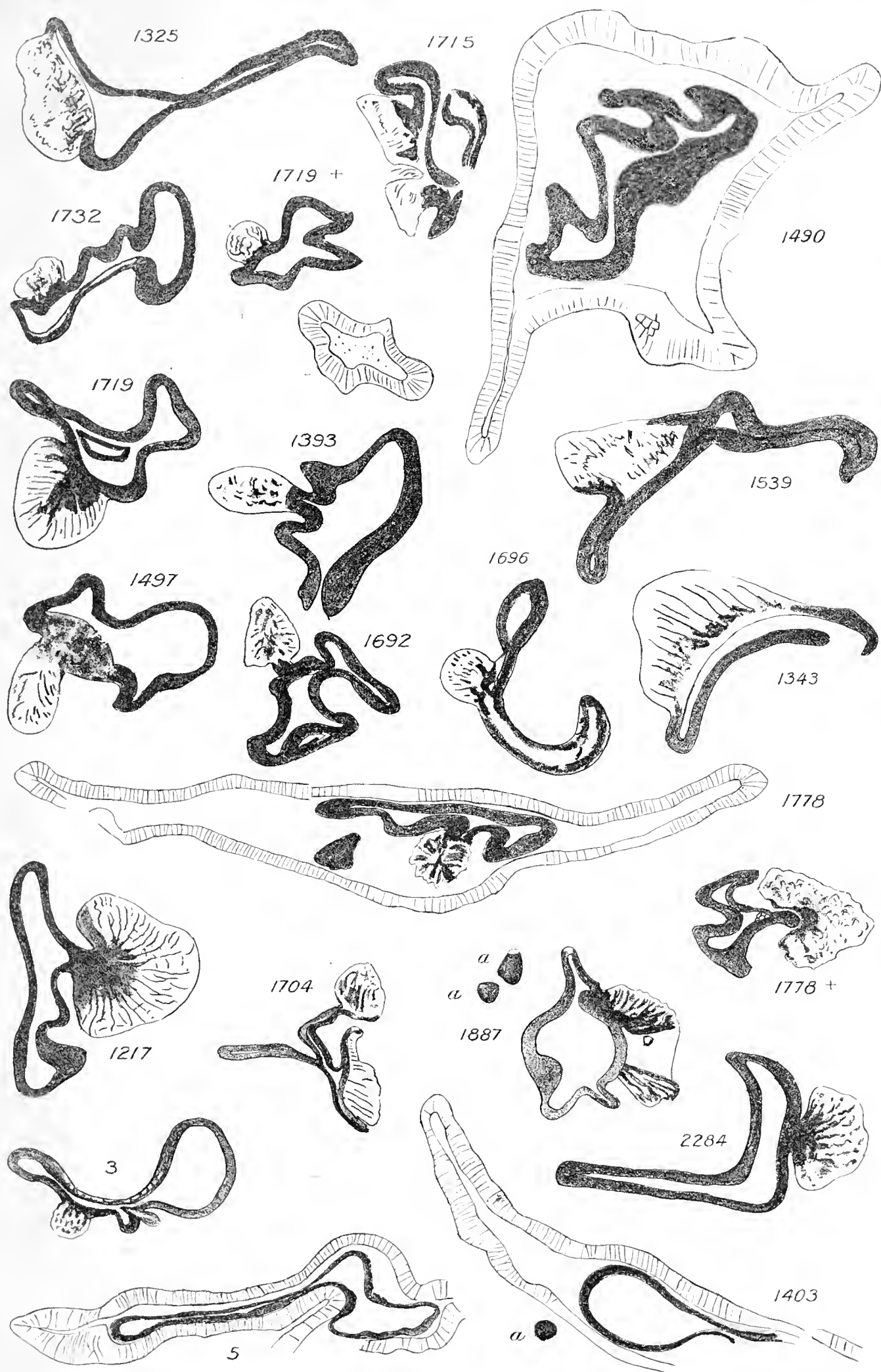
Fig. 3.



Fig. 4.

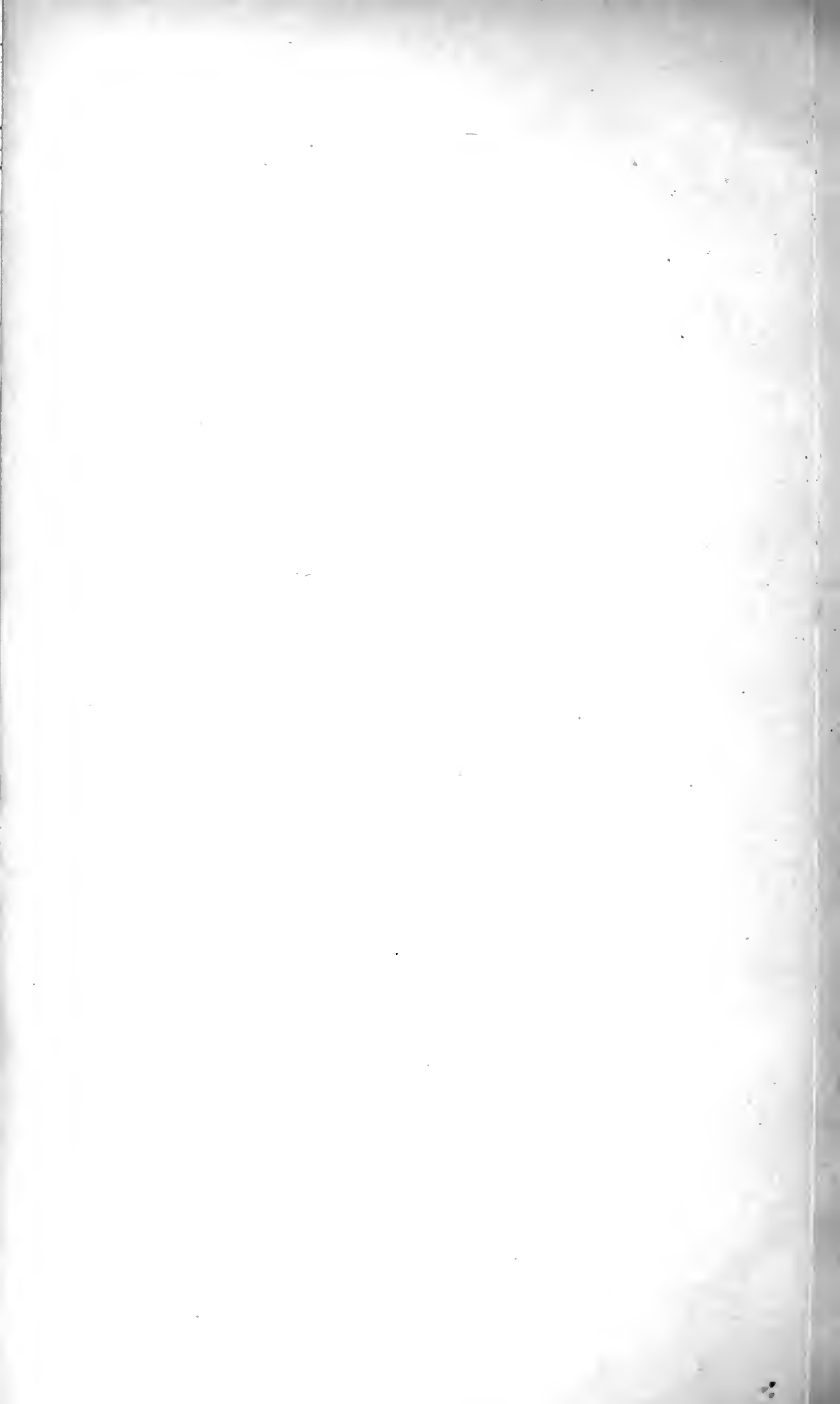
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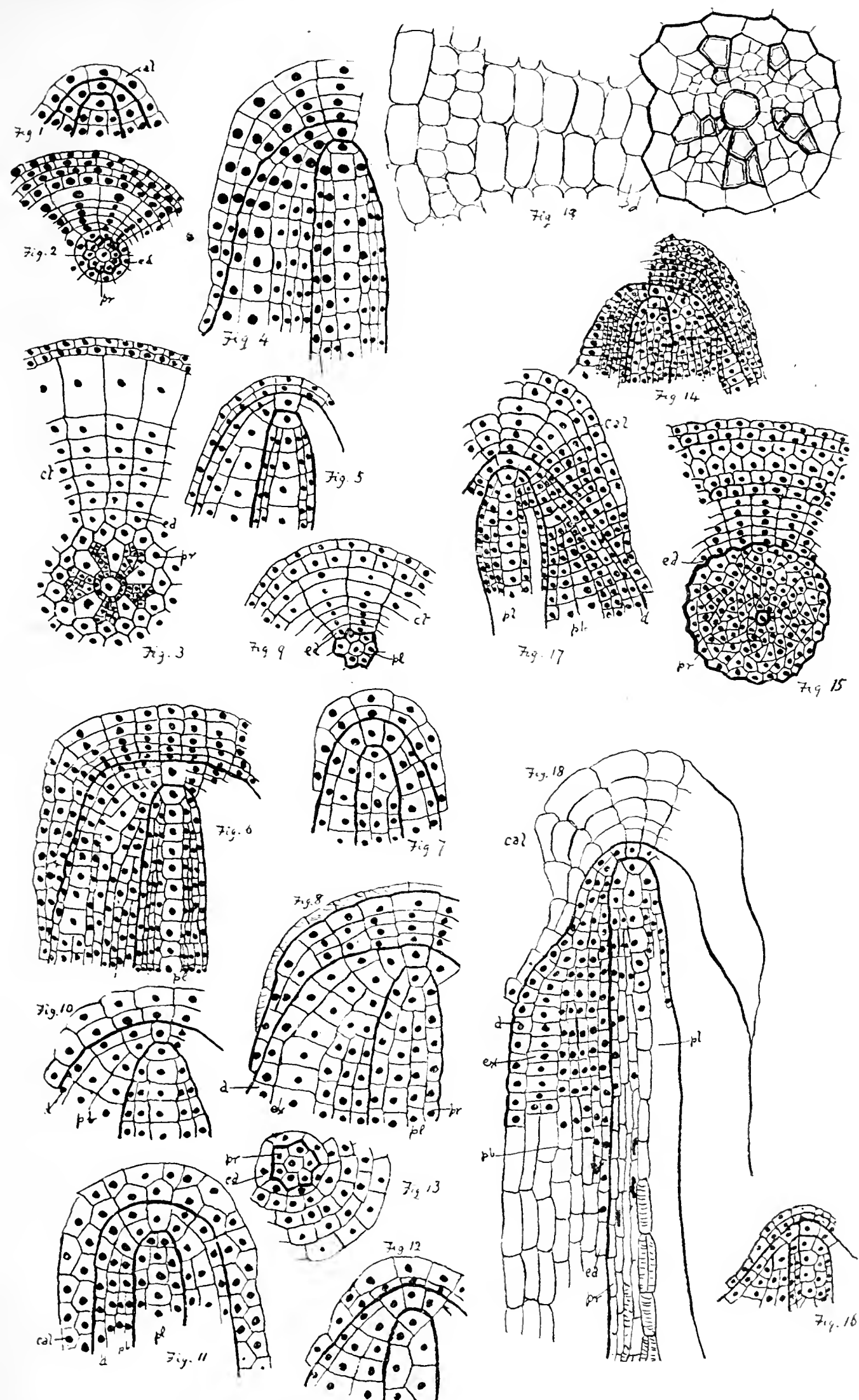




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# THE NEW PHYTOLOGIST.

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## SKETCHES OF VEGETATION AT HOME AND ABROAD.

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### III. "THE KARROO" IN AUGUST.

BY F. E. WEISS, D.Sc. AND R. H. YAPP, M.A.

[PLATES V., VI. AND VII., AND TEXT-FIGS. 15—23].

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ACCORDING to Bolus<sup>1</sup>, the Karroo region of Cape Colony is a broad, elevated tract of country, which stretches from the Ceres district on the west, to nearly as far as Grahamstown on the east. The altitude of this area varies from about 1,800—3,000 feet above the sea. Mountain ranges, trending east and west, bound the Karroo on the north and south. On the north the chief ranges are the Roggeveld, Nieuwveld and the Sneeuwbergen, while on the south are the Cederbergen, Cold Bokkeveld, Zwartbergen, Baviaans Kloof-bergen, etc.

Over the whole of this area the rainfall is small (indeed in some parts a whole year may occasionally pass without rain), while the daily range of temperature is very considerable. The severity of the climate, in fact, is such that the vegetation is of a desert or semi-desert character.

The following sketch is intended to give our impressions of the Karroo vegetation, as observed by us during a brief visit of some three or four days to the little village of Matjesfontein in August, 1905, just prior to the meetings of the British Association in Cape Town.

Matjesfontein is situated towards the west of the Karroo area as defined above, or almost on the extreme west of Dr. Marloth's "Central Karroo<sup>2</sup>." It is nearly 200 miles distant from Cape Town, some 2,970 feet above the sea, and lies on a gently undu-

<sup>1</sup> H. Bolus. Sketch of the Floral Regions of South Africa; in Science in South Africa. Cape Town, 1905, p. 223.

<sup>2</sup> R. Marloth. On the Phyto-geographical sub-divisions of South Africa. Brit. Association Report, South Africa, 1905.

lating plain, or plateau, several miles in width. This plain runs nearly east and west, and is bounded on the north and south by mountain ridges, probably 1,000 feet, or more, above the general level of the plain.

At Prince Albert, seventy miles further east, the mean annual rainfall is 11.49 inches,<sup>1</sup> though at Matjesfontein the precipitation is probably somewhat greater. Moreover, this part of the Karroo falls within the "Constant Rainfall Area<sup>2</sup>," which separates the western region of South Africa with winter rains, from the eastern district with over 70 % of its rainfall during the summer months. Thus Matjesfontein receives some part of its scanty rainfall during the winter months, and part during the summer. The rains are frequently reinforced by heavy dews, which are consequent on the rapid lowering of temperature at night.

The air on the Karroo, and this is also true of many other parts of South Africa, is as a rule, remarkably clear and bright, so clear as to render distances, at least to visitors from less sunny climes, very deceptive.

The tiny village of Matjesfontein is conspicuous from some distance, owing to the comparative luxuriance of its vegetation. The latter consists largely of plants belonging to the two Australian genera *Eucalyptus* and *Hakea*, together with (in the grounds of the Hotel Milner) a few orange trees. These plants can thrive here only by reason of frequent irrigation, which is effected by means of channels fed by pumping. The soil, however, is fertile enough, and it only needs a constant and sufficient supply of water to render it really productive.

Beyond the confines of the village, and as far as the eye can reach, the plain is covered with a low bush or scrub formation. Although the vegetation is intensely xerophilous in character, it is much more abundant than in many desert regions, such as the Sahara,<sup>3</sup> where the climatic conditions are still more severe. At a distance the scrub sometimes appears almost continuous (Fig. 1, Pl. V.), but a nearer view reveals the fact that the formation is really an "open" one, a considerable amount of bare soil or rock being visible (Figs. 1—3, Pl. V.)

The soil is stony, but finer particles, washed in between the

<sup>1</sup> Bolus. loc. cit., p. 224.

<sup>2</sup> C. M. Stewart. The Meteorology of South Africa. Science in South Africa, 1905, p. 28.

<sup>3</sup> See illustrations of the Algerian Sahara in A. F. W. Schimper's Plant Geography, 1903, pp. 608, et seq.



stones have given to the whole a hard caked surface. On the hillocks and kopjes, large boulders, and here and there ridges of bare rock, are abundant.

The mass of the vegetation is composed of dwarfed shrubs, about 2—3 feet (sometimes more) in height (Figs. 1—3, Pl. V.) Though these shrubs belong to many natural orders, their habit, as seen from a little distance, is remarkably uniform. For the most part they have a rounded outline, are richly branched, and usually possess leaves of an ericoid type. Such are *Galenia africana* (Fig. 3, Pl. V.), *Polygala teretifolia*, *Hermannia* sp., *Zygophyllum* sp. (Fig. 1, Pl. V.), and some Compositæ, e.g. *Elytropappus*.

Another very common type of shrub is that shown in Fig. 3, Pl. VII.; the woody stems are thick and gnarled, and project one or two feet from the soil, being crowned above with a dense tuft of small branches. *Pelargonium alternans* and many other plants show this peculiar habit.

The leaves and stems are often glaucous (*Zygophyllum* sp.), but sometimes (*Polygala* sp.) they are covered with short, felted hairs, giving a greyish aspect to the bush.

In addition to those mentioned above, succulent shrubs are fairly abundant. These possess the usual rounded outline, but instead of the narrow ericoid leaves, we find either thick, fleshy leaves, as in many species of *Mesembrianthemum* (Text-fig. 5, 19), *Cotyledon* (Fig. 2, Pl. VII.), *Aloë* (Fig. 1, Plate VII.), etc., or succulent water-storing stems, as in the species of *Mesembrianthemum* shown in Fig. 2, Pl. V., or in a large shrubby species of *Euphorbia*.<sup>1</sup>

The prevailing colour of the vegetation, at the time of our visit in August, was a dull greyish green, though distinctly greener than we had expected to see it. The colour, however, was by no means uniform. Here and there, where shrubs of *Galenia africana* (Fig. 3, Pl. V.), or the *Euphorbia* mentioned above, were numerous, the colour was a greenish yellow, while in such spots as that shown in Fig. 2, Pl. V., the green hue was almost entirely lost, the stems of the *Mesembrianthemum* shown in the foreground, imparting a bleached, grey appearance to the scene.

Here and there the general level of the plain is interrupted by water-courses. The latter, at the time of our visit, usually contained little, if any, water, but were easily recognisable, even from a distance, by the low trees or larger shrubs which fringe their banks (Figs. 1, 2, Pl. VI.) These dwarfed trees were, for the most

<sup>1</sup> A small specimen of this *Euphorbia* is seen on the left of Fig. 1, Pl. VII.

part, either *Rhus viminalis* or *Acacia horrida*, the latter often forming impenetrable clumps of "thorn-bush" (Fig. 3, Pl. VI.). The only other shrub which appeared to rise conspicuously above the general level of the surrounding vegetation was *Euclea undulata*, which we found occasionally on rising ground.

Near the village, in the water-courses themselves, occurred extensive growths of the introduced *Gomphocarpus fruticosus*, with willow-like leaves.

Probably the great majority of the plants mentioned hitherto, depend largely on subterranean sources, so far as their water supply is concerned.<sup>1</sup> But in between the more conspicuous shrubs many smaller plants occur, which are more directly dependent upon the surface water available after showers of rain. The latter include (i.) many of the smaller succulents; (ii.) plants with underground storage-organs, the aerial parts of which disappear during the dry season; and (iii.) annuals, the vegetative period of which is extremely short, the dry season being passed in the form of seeds.

(i.) Succulent plants form a far more important feature of the Karroo vegetation, than of that of the deserts of North Africa. In fact, they comprise in some districts of the former more than 33% of the total phanerogamic vegetation.<sup>2</sup> In addition to the shrubby succulents mentioned above, herbaceous forms, often only a few inches in height, abound; e.g., different species of *Crassula*, small *Mesembrianthemum*, Compositæ with fleshy stems or leaves (Text-Fig. 4).

(ii.) The aerial parts of plants with fleshy roots, tubers, bulbs and other subterranean storage organs spring up abundantly after the rains. Such are some Compositæ, various species of *Oxalis*, and numbers of Monocotyledons (*Bulbine*, *Babiana*, *Moraea*, etc.) The latter plants appeared to occur more especially on the comparatively low ground, rather than on the kopjes.

In many places shallow channels, half an inch to an inch in depth, and perhaps a foot or so broad, had been excavated in the bare sandy soil, evidently by the rush of water during heavy rains. We noticed in many instances that these little channels (quite dry during our visit) contained numbers of *Moracae*, while few or none were to be found on the surrounding soil, though the level of the latter was only very slightly above that of the channels themselves. In other cases the *Moracae* occurred in more extensive patches in

<sup>1</sup> Schimper, loc. cit., pp. 612, et seq.

<sup>2</sup> A. Engler, Ueber die Frühlingsflora des Tafelberges bei Kapstadt. Notizblatt d. Königl. bot. Gart. u. Museums zu Berlin. Appendix XI., April, 1903, p. 42.

places where the general soil level was slightly depressed (Fig. 4, Pl. VII.). Perhaps the explanation in both cases is to be found in the fact that during rain the water would collect in these shallow channels or depressions, and thus more would soak in to the depth at which the tubers and bulbs are buried, than would occur in soil from which the water could run off more readily. Thus the plants in these relatively favoured spots might spring up under the influence of showers insufficient to induce the growth of those in somewhat drier situations.

(iii.) In some places numbers of pretty little annuals were found, either in the shelter of the larger bushes, or, here and there, sufficiently abundant to form dense patches of green sward. The dark foreground in front of the *Zygophyllum* bushes in Fig. 1, Pl. V.,



Fig. 15.



Fig. 16.



Fig. 17.

Fig. 15. *Heliophila* sp. Fig. 16. *Cotula* sp. Fig. 17. *Diascia Sacculata*.  
(All slightly reduced.)

consists of one of these sward-like patches of annuals. Flowers and even fruits may frequently be seen on seedlings only an inch or two in height, and on which the cotyledons are still fresh and green (see Text-figs. 15—17). As Warming<sup>1</sup> remarks, the adaptation which these ephemeral species exhibit to the dry climate, lies in the short duration of their lives, which are thus passed wholly under favourable conditions.

The slopes of the two ranges of hills which form respectively

<sup>1</sup> Eug. Warming, *Lehrbuch der ökologischen Pflanzengeographie*, 1896, p. 253.

the northern and southern boundaries of the plain around Matjesfontein, exhibit considerable differences, even as seen from a distance. Those of the Witteberg range (seen in Fig. 3, Pl. V. and Fig. 1, Pl. VI.), lying to the south, and thus facing the more intense northern illumination, are more arid and devoid of vegetation than the slopes of the kopjes lying to the north (Fig. 1, Pl. V.), and thus facing south.

Unfortunately we were unable to visit the summits of the higher and more distant ridges, and had to content ourselves with exploring a few of the nearer and lower kopjes. Soil is less abundant on these kopjes than on the plain, and bare rock often covers much of the surface of the ground. Consequently the vegetation is, if possible, still more markedly xerophilous. Thus, annuals seemed to be almost entirely absent on the hills, while succulents (*Aloe*, *Haworthia*, *Euphorbia*, etc.) became an even more prominent feature of the vegetation (Fig. 1, Pl. VII.) On one of the higher ridges visited (a northern outlier of the Witteberg), we found a Restionaceous plant in some abundance. Dr. Marloth tells us that the flora of the mountain ridges of this region shows some affinity to that of the South-Western region; as not only Restionaceæ, but Proteaceæ and other characteristic Cape forms occur on these ridges.

Of cryptogamic plants, lichens were undoubtedly the most conspicuous, the bare rock surfaces on both hills and plain being frequently almost covered with patches of lichens: bright red (*Amphiloma*), yellow (*Parmelia*), or grey (*Urceolaria*, etc.) in colour.

A few hardy ferns (such as *Ceterach capensis*, *Cheilanthes hirta*, etc.), some small moss-cushions, and even liverworts were found. These appeared to occur most frequently in the more shady and sheltered spots, under overhanging rocks, etc., particularly on the southern sides of the kopjes.

In comparison with other desert areas, not only do the presence of large numbers of succulents, as well as of bulbous and tuberous plants, form a very marked feature of the Karroo, but the systematic composition of the phanerogamic vegetation appears to be considerably richer in the Karroo area than in many other deserts.<sup>1</sup>

Bolus<sup>2</sup> has given a table showing the dominant orders occurring in the Karroo region, with the number of species in each. According to him there are in all some eighty-four natural orders, represented by

<sup>1</sup> Warming, loc. cit., p. 253, and Schimper, loc. cit., p. 630.

<sup>2</sup> Bolus, loc. cit., p. 225.

about 1,344 species. But probably many Karroo plants have yet to be described, as during even the few days of our visit, we collected a number of plants which have since turned out to be new species.

It may be of some interest if we give our own impressions regarding some of the more striking orders and genera which we observed at Matjesfontein, impressions which were necessarily determined to a large extent by those plants which happened to be in flower at the time.

The Compositæ were, without doubt, the most conspicuous family, not only as regards the number of individuals and species, but also in respect of the great variety of habit represented by these species. Thus, amongst shrubby Compositæ, with leaves more or less of the ericoid type, are *Eriocephalus glaber*, *Relhania*, n. sp., and *Euryops* (*E. asparagoides* ?); *Elytropappus* is a tamarisk-like shrub with cupressoid leaves. Herbaceous composites were also very abundant, such as *Kleinias* with succulent stems, and

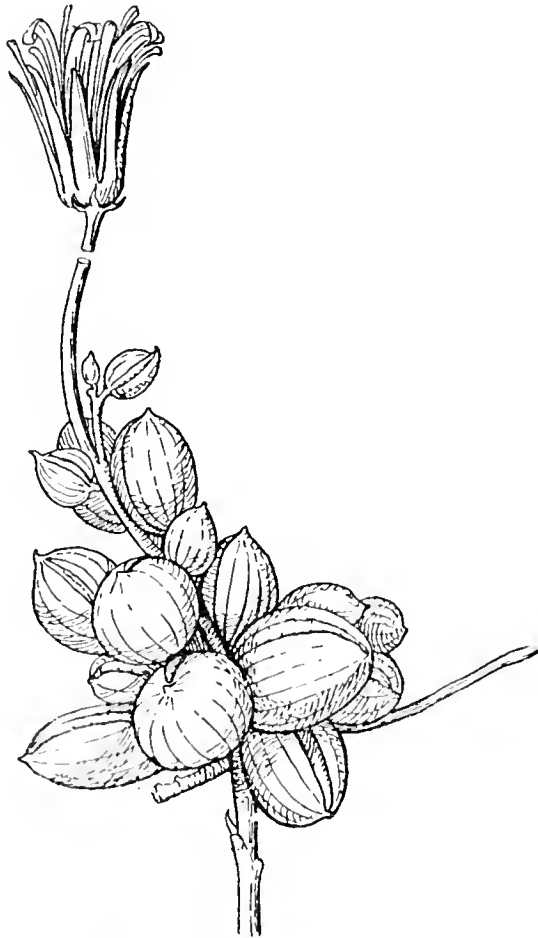


Fig. 18. *Othoma* sp. Slightly reduced.

*Othomas* with globular succulent leaves (Text-fig. 18). Others had underground tuberous stems; some had the habit of a *Gerbera*, with radical pinnatisect leaves, and no marked storage organs, while others again were annuals (Text-fig. 16).

Next to the Compositæ must be mentioned the Aizoaceæ. According to Bolus<sup>1</sup> this family, which is chiefly a South African one, forms about 8.3% of the whole Karroo flora, the chief genus alone, *Mesembrianthemum*, being represented by seventy species. Many of the low-growing species of this genus were flowering during August, the patches of crimson, pink or yellow flowers forming a brilliant contrast to the prevailing dullness of the vegetation.

With the exception of *Galenia africana* (Fig. 3, Pl. V.), a much branched shrub with ericoid leaves, those members of this family which we observed were succulents belonging to the genus *Mesembrianthemum*. Some were shrubs of a considerable size, e.g., the species with succulent stems and reduced leaves seen in Fig. 2, Pl. V., and *M. spinosum*, with succulent leaves and a spiny inflorescence (Text-fig. 19). *M. minimum* is another interesting species with its diminutive shoots and connate pairs of leaves.<sup>2</sup>

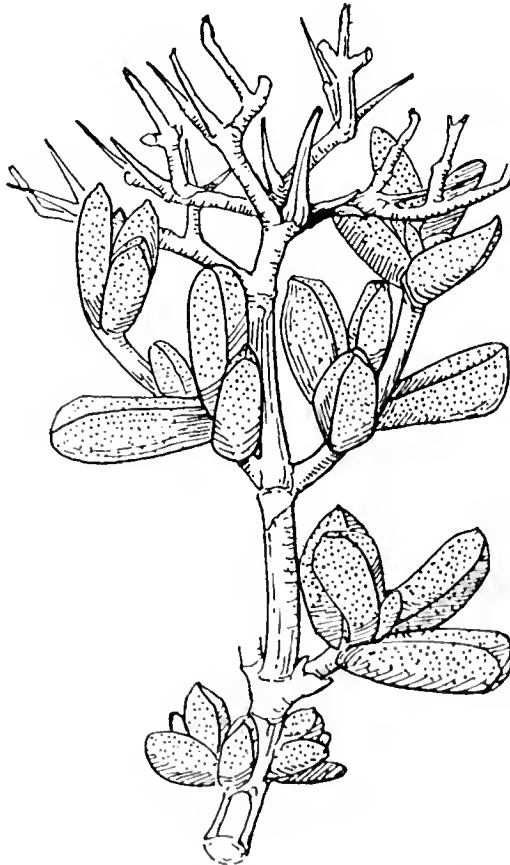


Fig. 19. *Mesembrianthemum spinosum*. (Slightly reduced).

One species of *Mesembrianthemum* had a thick, fleshy tap-root, while another showed two distinct root-systems (Text-fig. 20). One

<sup>1</sup> Bolus, loc. cit., pp. 225-6.

<sup>2</sup> This species has the habit of *M. obconellum*, see figures and description of the latter in Goebel, Pflanzenbiologische Schilderungen, Part I., p. 49, Figs. 21 and 22.

of the root-systems of the latter species descends vertically into the soil in the ordinary way, while the other, which consists of roots given off laterally near the base of the main root, spreads horizontally just under the surface of the soil. It would seem probable that this horizontal root-system is more especially concerned with the absorption of moisture available after slight

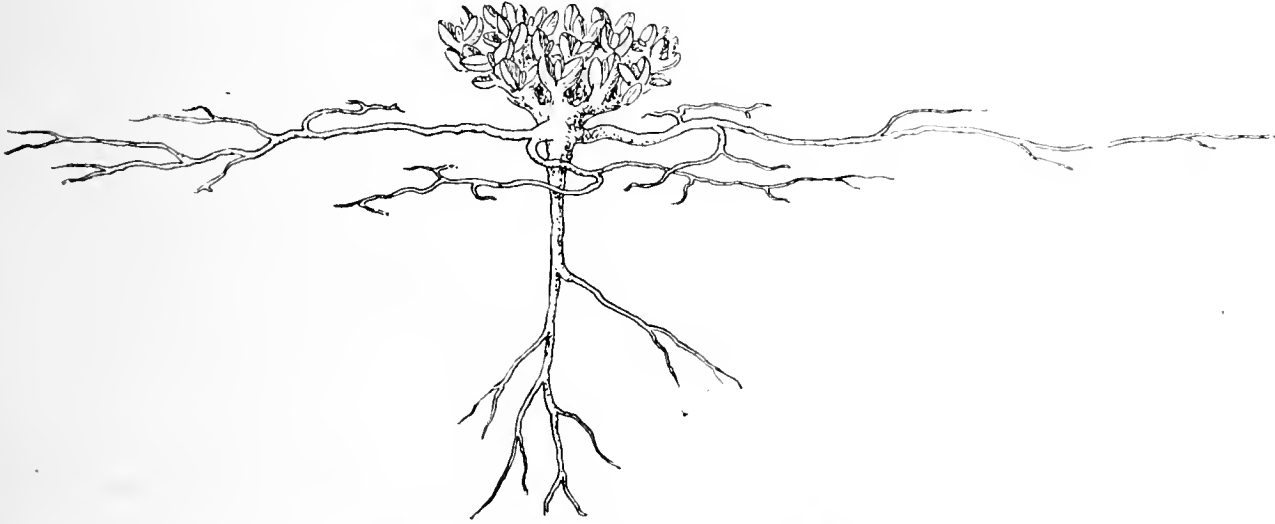


Fig. 20. *Mesembrianthemum* sp. (About one half natural size).

showers, or heavy dews, and which would scarcely soak in to a sufficient depth in the soil to be absorbed by a vertical root-system. Such is the explanation given by Volkens<sup>1</sup> of the superficial lateral roots of species of *Diploaxis* and *Euphorbia* found in the Egyptian deserts. We also noticed a similar horizontal spreading of the roots in a species of *Bulbine* (Text-fig. 23).

The Crassulaceæ exhibit some remarkable succulent forms. Especially prominent are three shrubby species of *Cotyledon*. Of these, *C. fascicularis*<sup>2</sup> is the largest. It attains a height of some three to four feet, and has enormously thick stems. The stem of one large specimen which we measured, had a girth of 3 feet 11 inches. On account of the extreme softness of these large water-storing stems, the plant is locally known as the “Butter-tree.”

*C. Eckloniana* is another striking species (Fig. 2, Pl. VII.) In both these species, and also in the smaller *C. reticulata*, the axes of the inflorescence, and frequently the dry, opened fruits, persist after flowering (see figures cited above). In the latter species they become considerably hardened, and form a fairly dense network, which spreads as a canopy over the foliage beneath. Possibly this

<sup>1</sup> G. Volkens, Die Flora der Ägyptisch-Arabischen Wüste, Berlin, 1887, p. 24.

<sup>2</sup> Several plants of this species are to be seen in the foreground of Fig. 1, Pl. VI.

network of axes and fruit-remains may afford some protection to the young developing leaves of the plant (for *C. reticulata*, like the other two species, periodically sheds its leaves), from the intense direct illumination of the desert sun.<sup>1</sup>

The genus *Crassula* was also much in evidence. *Crassula pyramidalis* is a dwarf form with numerous closely imbricated leaves, surmounted by a tuft of sweet-scented white flowers. Its local name of "shaving-brush" gives a good idea of the general appearance of the plant when in flower.

*C. columnaris* is a shorter and broader form, whose pebble-like appearance, and dull colouration, have given rise to the suggestion that it may be protected from herbivorous animals by its close resemblance to rounded stones.<sup>2</sup> *C. lycopodioides* has, as its name suggests, a habit resembling that of some Lycopodia. Another *Crassula* (*C. monticola*?) was a woody shrub, with thick button-like leaves. Several other species of *Crassula*, and amongst them one or two new species, were found; one of the latter was apparently an annual, with a pair of large flat leaves, growing amongst mosses and liverworts in a few shady, sheltered spots.

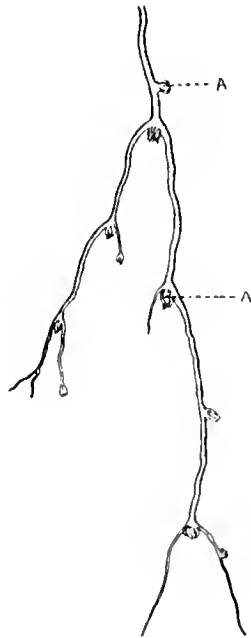


Fig. 21. Root of *Crassula* sp.

The roots of all the Karroo Crassulaceæ which we examined, had one striking feature in common. As seen with the naked eye,

<sup>1</sup> Cf. the "paraheliodes" of Darbshire. Observations on *Mamillaria elongata*, Annals of Botany, 1904, Vol. XVIII., p. 404.

<sup>2</sup> R. Marloth. Trans. S. Afr. Phil. Soc., 1905, p. 165. Cf. also descriptions and photographs of S. African species of *Mesembrianthemum*, etc., which are said to show protective adaptations, in a paper by Sir W. T. Thiselton-Dyer, Ann. of Botany, 1906, Vol. XX., pp. 123, et seq.



the roots appeared to possess a number of tiny lateral buds. A closer examination showed that the “buds” consisted of little tufts of short lateral rootlets, evidently of limited growth (Text-fig. 21A). Since our return from South Africa, we have found a somewhat similar arrangement of lateral rootlets in a number of the British members of the order. A fuller investigation into the origin, structure, etc., of these lateral root-tufts of the Crassulaceæ is in progress, and we hope before long to be able to publish a more detailed account.

The Euphorbiaceæ are conspicuous, though not a dominant order as regards the number of species, as only seventeen have hitherto been recorded from the Karroo region.<sup>1</sup> *Euphorbia Hystrix* is a species with long axillary shoot spines, to be met with on kopjes, amongst the rocks. The commonest species, however, appeared to be a bushy, much-branched, spineless form, which frequently stands five feet high. This plant is yellowish-green in colour, and, in places where it is abundant, imparts that hue to the vegetation. A small specimen is seen on the left of Fig. 1, Pl. VII. We saw, at Matjesfontein, no tree-Euphorbias of the type of *E. grandidens*, which so often form such a characteristic feature of the vegetation in South Africa (we frequently saw these big tree-Euphorbias in Natal, the Transvaal and also in Rhodesia).

Very few Geraniaceæ were in flower in August, and so they largely escaped our notice. *Sarcocaulon Burmanni* (Text-fig. 22), an interesting succulent with spinose leaves, may, however, be mentioned; also *Pelargonium alternans*, a woody plant of somewhat the same habit as the shrubs shown in Fig. 3, Pl. VII.

Amongst monocotyledons the Iridaceæ and Liliaceæ were the dominant orders.

Of the former may be mentioned several species of *Moraea*, with white or yellow flowers (Fig. 4, Pl. VII.). The white-flowered *Moraea* appeared to open its flowers only after mid-day. A *Babiana* with fine blue flowers, and two white-flowered species of *Lapeyrousia* (*L. caespitosa* and *L. fistulosa*) were also found.

The Liliaceæ were represented by the genera *Bulbine* (Text-fig. 23); *Asparagus*; *Massonia*, with its single pair of large leaves, closely appressed to the soil; *Aloe* (Fig. 1, Pl. VII.); *Harworthia*; *Gasteria*, etc., the three latter with large succulent leaves.

Very few grasses were seen, and very few leguminous plants, though the Gramineæ and Leguminosæ are, according to Bolus,<sup>1</sup> two of the largest Karroo orders.

<sup>1</sup> Bolus, loc. cit., p. 225.

In addition to the features already mentioned, a few others call for attention.



Fig. 22. *Sarcocaulon Burmanni* (slightly enlarged).

#### SPINY PLANTS.

The first of these is the spiny habit, which many of the Karroo plants, in common with those of other desert regions, possess.

The spines may be of very different morphological nature in different cases. Thus, in *Acacia horrida* they are well-developed stipules, in *Sarcocaulon Burmanni* (Text-fig. 22) they are modified leaves. Whole axillary shoots become thorns in *Asparagus* sp., and *Euphorbia Hystrix*.<sup>2</sup> In *Mesembrianthemum spinosum* (Text-fig. 19) it is some of the inflorescence axes which become modified as spines.<sup>3</sup>

While we do not wish to attempt the solution of the vexed question as to whether spines are to be looked upon as reduced structures, correlated with, and produced by, dryness of climate or other purely physical factors; or, on the other hand, as organs of

<sup>1</sup> Bolus, loc. cit., p. 225.

<sup>2</sup> In most spiny Euphorbias the thorns are paired stipules; in *E. hystrix* their morphological value is the same as in *E. mamillaris*, see Goebel, loc. cit., part I., p. 62.

<sup>3</sup> Chodat, in "Une excursion botanique à Majorque" 1905, p. 81, describes a spiny inflorescence in *Sonchus cervicornis*.

protection, produced through the agency of natural selection, we may perhaps point out that in *Acacia horrida* at least (and also in other South African species of *Acacia*), the stipular spines, instead of being reduced, are really highly developed structures, often several inches in length. These spines, moreover, with their white, glistening appearance, are very conspicuous objects. Then again, the spines on the lower branches were, on the plants we observed, larger and more formidable than those on the upper<sup>1</sup> (Fig. 3, Pl. VI.). These facts tend to show that, however these *Acacia* spines may have arisen, they form at the present time an efficient protection against the attacks of most of the larger animals.

Perhaps the mean between the two views cited above is nearer the truth than either taken alone. Thus, supposing the spines in a given case to have originated in response to physical environmental conditions; then, if they were even of a slight protective value at this early stage, their subsequent phylogenetic development may well have been guided, or at least assisted by natural selection. Herbivorous mammals, feeding by preference on the less spiny forms, may thus have been, at least in some cases, one of the factors contributing to the degree of spinosity, though not to the formation of spines in the first instance.

Beecher<sup>2</sup> believes that “in every case no single reason is sufficient to account for this spinose condition. The original cause may not be operative through the entire subsequent phylogeny.”

Another factor which may cause the retention and possibly the further development of spinescent structures is the very intense illumination to which these Karroo plants are exposed. We have hinted in the case of *Cotyledon reticulata* at the possible screening effect of the hardened and persistent remains of the inflorescence, which forms a dense network over the tender foliage of the plant. Similarly the spiny hairs of a species of *Mesembrianthemum* we found are probably too weak to act as a defensive mechanism, but resembling as they do in their arrangement, the tuft of spiny hairs at the end of the leaf of *Mesembrianthemum stellatum*, they

<sup>1</sup> One of us has observed the same phenomenon in an even more marked degree, in the eastern *Bambusa spinosa*, whose lower branches form an impenetrable spiny thicket, while the upper are entirely free from thorns (R.H.Y.). Cf. also the more spiny leaves often found on the lower, than on the upper branches of the holly.

<sup>2</sup> C. E. Beecher. *Studies in Evolution*, New York, 1901, p. 4. Though he is here referring more especially to animals, it is probably equally true of plants.

may act as Darbshire<sup>1</sup> has suggested in the case of the latter as "paraheliodes."

#### SPIRALLY-TWISTED LEAVES.

Another noticeable feature was the spiral twisting which the linear leaves of many Monocotyledons (Liliaceae, etc.) appeared to have undergone. Sometimes each leaf was twisted into a spiral

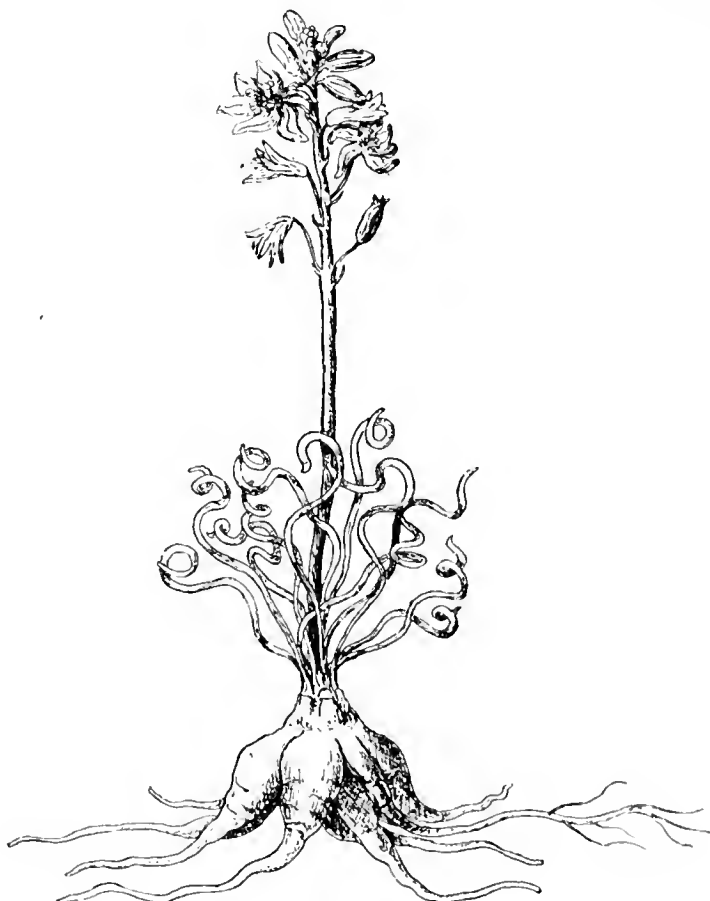


Fig. 23. *Bulbine* sp.

independently of its fellows, e.g., *Bulbine* sp. (Text-fig. 23)<sup>2</sup>, while in other cases all the leaves of a plant seemed to have been twisted simultaneously.

We noticed a similar, though less well-marked, tendency to spiral twists in the leaves of several plants on Table Mountain, in the Cape Peninsula; notably in a grass and in the linear leaf-segments of a species of *Oxalis*.

#### SCENT, ETC., OF FLOWERS.

The great majority of the flowers which we saw at Matjesfontein, had a strong and sweet perfume.

With regard to the colours of the flowers in bloom in August,

<sup>1</sup> O. V. Darbshire. Loc. cit., p. 412.

<sup>2</sup> Cf. also plates 259 and 260 in Baker's Monograph of the genus *Gethyllis*, Jour. of Botany, Vol. XXIII., 1885.

yellow appeared to be the dominant colour, then white, then red, while only a very few blue flowers were observed.

One or two observations were made on insect and other visitors to flowers. A tall *Senecio* was systematically visited by a dipterous insect belonging to the Bombylidae, and also by a very hairy beetle of the genus *Hoplia* (Cetoniidae). The spineless *Euphorbia*, shown on the left of Fig. 1. Pl. VII., was visited by numerous small beetles also belonging to the Cetoniidae.

Just before the photograph forming the last mentioned figure was taken, one of us noticed a sun-bird, with bright metallic green plumage (probably the Malachite sun-bird, *Nectarinia famosa*) sucking honey from the flowers of the *Aloe* shown in the middle of the photograph.<sup>1</sup>

Our best thanks are due to Dr. H. Bolus, Lieutenant-Colonel Prain (Director of the Royal Gardens, Kew), Mr. N. E. Brown, and Dr. O. V. Darbishire, for their kind assistance in identifying some of the plants mentioned in this paper. We also desire to express our indebtedness to Miss Emily Dust for executing the drawings which constitute Text-figures 15—19 and 22.

<sup>1</sup> Cf. G. F. Scott-Elliot. Ornithophilous Flowers in South Africa. Annals of Botany, 1890, Vol. IV. pp. 265 et seq.

## EXPLANATION OF PLATES V., VI. AND VII.

### PLATE V.

- Fig. 1. General view of Karroo vegetation near Matjesfontein, looking nearly east. In the foreground is a sward-like patch composed of annuals; behind this are bushes of *Zygophyllum* sp.—further in the distance are seen *Elytropappus*, etc.
- Fig. 2. The dominant shrubs here are a species of *Mesembrianthemum* with fleshy stems and reduced leaves.
- Fig. 3. Facing the Witteberg range. *Galenia africana* dominant.

### PLATE VI.

- Fig. 1. On high ground near foot of the Witteberg. In the centre is a stream bed—whose course is faintly indicated by the somewhat greater size of the shrubs. In the foreground are several specimens of *Cotyledon fascicularis*.
- Fig. 2. Watercourse on plain, note the larger trees (*Rhus viminalis* and *Acacia horrida*) fringing its banks.
- Fig. 3. *Acacia horrida*.

### PLATE VII.

- Fig. 1. Summit of small kopje lying south of Matjesfontein. *Aloe* sp. in centre; to right of this, and again on left of photograph, are seen the small cylindrical stems of some small specimens of a common *Euphorbia*.
- Fig. 2. *Cotyledon Eckloniana*, on summit of a low kopje.
- Fig. 3. A common type of woody shrub found on the Karroo.
- Fig. 4. A white flowered species of *Moraea*.

ON THE MEGASPORE OF *LEPIDOSTROBUS*  
*FOLIACEUS*.

BY RINA (MRS. D. H.) SCOTT, F.L.S.

[WITH PLATE VIII. AND TEXT-FIGS 24, 25.]

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DR. SCOTT has recently been revising the catalogue of his collection of fossil plants from the coal measures and in looking through the slides one's eye gradually became impressed with the presence in many of the sections from Dulesgate and the Halifax hard bed of a curious looking, very badly preserved, black object, like a much crumpled spore with an appendage attached to it (Text-fig. 24, and Plate VIII., 1217).<sup>1</sup>

It was not until 1325 slides had been searched, that I came to the conclusion, that this object was of the nature of a spore and worth investigating.

I drew each specimen found with the camera lucida and became more and more convinced that it was really a megaspore and not, as one might easily think at first sight, a badly preserved petiole or stem. Also it soon became evident that the appendage was a definite structure, less altered in the course of preservation than the megaspore to which it belonged. I was strengthened in my opinion that it was a megaspore by finding a specimen (Plate VIII., 1490) in a sporangium, though the appendage was not shown.

Up to the present, I have found over 40 specimens in 1500 slides, so that it may be looked upon as a fairly common object; I hope that the megaspores drawn on Plate VIII may help others to find fresh examples.

1704 (Plate VIII) appears to possess two appendages, this I think is due to the twisting of the megaspore so that one part of the appendage is cut at right angles to the other.

I had temporarily given the name of *Triletes diabolicus* to this specimen: *Triletes* being the general name used by Mr. Kidston for megaspore and *diabolicus* explains itself when one has seen the object.

Let us now examine the megaspore in more detail. It is not easy to decide whether it was spherical or egg-shaped, but on measuring round the outline of a camera lucida drawing with thread, I find that the diameter of a sphere would be about 1.5 mm.

<sup>1</sup> The numbers given in connection with the figures are the cabinet numbers of the slides in Dr. Scott's collection.

From such measurements as it has been possible to make, there were probably several, perhaps four, megaspores in each sporangium.

Turning to the appendage it seems clear, that in Plate VIII., 1719 and 1217, where the veins are radiating out from the point of attachment, are sections through the appendage in *one* direction,



Fig. 24. Photograph of 1217 (Plate VIII.)

while 1539, 1343 and 1715 are cut at a plane at right angles to the former, and the veins are cut vertically. In 1715 there appears to be a cleft filled by hairs, which may be where the microspores gained access to the megaspore. In 1887, a much less well-preserved specimen, there are microspores in the cleft. At *a, a*, these microspores are shown enlarged.

I have made a model of the appendage and spore, which appears to explain the appearance of the different sections. It reminds one of the so-called "swimming-apparatus" of *Azolla*.

The appendage was evidently a fairly substantial structure, which resisted distortion much better than the megaspore itself.

The nature of the structure cannot be determined, but it is not cellular and its appearance indicates, that it was part of the cell-wall probably derived from the tapetal protoplasm.

There is some evidence of this origin in the case of the bristles of other megaspores.

While examining *Lepidostrobus foliaceus*, further details of which will be found in Mr. Maslen's<sup>1</sup> paper on *Lepidostrobus*, I came across megaspores of this plant in their sporangium in connection with the characteristic bract (Plate VIII., 5 and 1403 and Text-fig. 25). This point is of especial interest as up till now the cone has always been considered homosporous<sup>2</sup>.

We must turn to Professor Williamson's splendid specimen of

<sup>1</sup> On the Structure of *Lepidostrobus*. Trans. of the Linnean Society. Vol. V. 1899, P. 373, Plate 38, Figs. 36—39.

<sup>2</sup> On the Organization of the Fossil Plants of the Coal-Measures, Part XIX. Phil. Trans. Royal Society, Series B. 1893, P. 27, Plate 9, Fig. 57.

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the microsporangiate cone of this plant in order to understand the details of its structure. The original slide is in the Natural History Museum, C.N. 1614. This is the type specimen on which Mr.

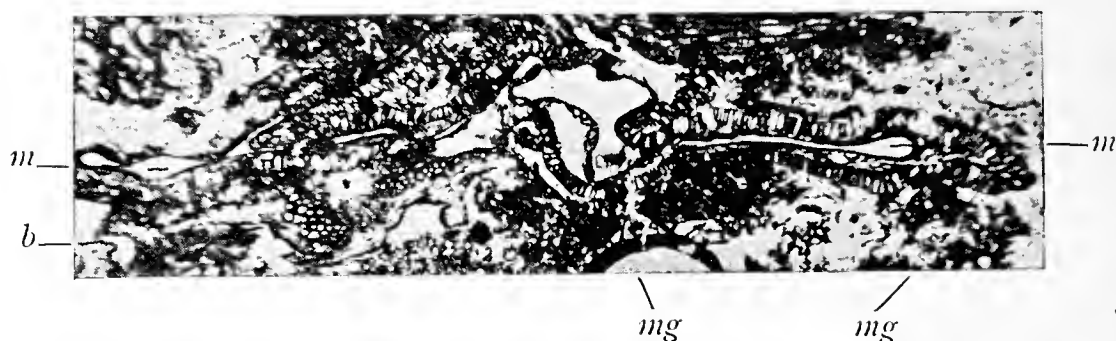


Fig. 25. Photograph of 5 (Plate VIII.) Sporangia containing megaspores, one with the characteristic braet of *Lepidostrobus foliaceus*.

*m.*, megaspore. *mg.*, megasporangium. *b.*, braet.

Maslen founded his species *Lepidostrobus foliaceus*. The section is a fairly radial one through the microsporangiate part of the cone. It is not quite median but it clearly shows the elongated form of the sporangia seated on the sporophylls with their leaf-like laminac from which the specific name was taken.

We have been trying for the last year to sort out the different megaspores of *Lepidostrobus*, so I looked through our camera lucida drawings of megaspores to match those found in the sporangia.

The result was, that the only ones at all corresponding in size and texture were my other new megaspores *Triletes diabolicus*. I searched carefully to see if I could find any sign of the curious appendage, but without success, till when 1778 was reached I had the good fortune to find a sporangium containing a typical *Triletes diabolicus*.

Since then I have been through every slide of *Lepidostrobus foliaceus* and have found that 25 out of 36 show the *Triletes*. I now thought if the type cone of Williamson were examined and showed *Triletes diabolicus* in the cone the evidence would be conclusive.

The cone, however, so far as shown, is purely microsporangiate, but the section shows a very fine specimen of *Triletes diabolicus* completely enclosed in a sporangium, identical in appearance with those containing the microspores, so that I think there is little doubt that the two new megaspores are really one and the same, that the Williamson cone must in future be considered as a heterosporous not a homosporous one and that *Triletes diabolicus* must disappear and become the megaspore of *Lepidostrobus foliaceus*.



I am indebted to Mr. L. A. Boodle for the photographs reproduce in Figs. 24 and 25.

The Figures on Plate VIII. are from my own drawings.

DESCRIPTION OF FIGURES ON PLATE VIII., ILLUSTRATING  
MRS. D. H. SCOTT'S PAPER "ON THE MEGASPORE OF  
*LEPIDOSTROBUS FOLIACEUS*."

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Drawings of megaspores of *Lepidostrobos foliaceus*, showing the appendage. The numbers are those of the slides in Dr. Scott's collection. 1490 shows a megaspore in a sporangium. 5 is represented in the photograph Fig. 25. 1217 is represented in the photograph Fig. 24.

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THE APICAL MERISTEMS OF THE ROOTS OF  
CERTAIN AQUATIC MONOCOTYLEDONS,

BY DAISY G. SCOTT, B.Sc.

(University of Liverpool).

[PLATE IX.]

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THE mode of origin of the permanent tissues from the apical meristem in the root of the Monocotyledon has been the subject of investigation at the hands of many anatomists. The results arrived at have been summarised more especially by two authorities, *viz.* : by De Bary in his "Vergleichende Anatomie der Vegetationsorgane der Phanerogamen und Farnen," 1877, (English Edition, 1884), and by Van Tieghem in "L'origine des membres endogenes," 1889. These views may be expressed briefly as follows :—

De Bary considers that there are two types of structure in the apices of the roots of Monocotyledons: (*a*), a type found in very few Monocotyledons, in which there are four initial layers giving rise respectively to (1) the plerome, (2) the periblem, (3) the dermatogen, and (4) the ealyptragen and (*b*), a type found in the majority of Monocotyledons, in which there are three sets of initials giving rise respectively to (1) the plerome, (2) the periblem and dermatogen together, (3) the ealyptragen. De Bary further holds that the epidermis is always a single layer, and that this layer originates separately or from a common group with the periblem.

Van Tieghem, with but few exceptions, considers that the mode

of origin of the tissues of all roots, whether of Dicotyledon or of Monocotyledon, is the same, each root having three sets of initials which give rise respectively to (1) the pterome, (2) the cortex, (3) the epidermis (= root-cap). He holds that the epidermis is many layered at the apex and that the external layers act as a root-cap, while the outermost central cells furnish the piliferous layer.

In the following notes an attempt is made to determine the mode of origin of the different embryogenic layers in the roots of the following genera of Monocotyledons, viz.:—*Alisma*, *Butomus*, *Vallisneria*, *Ruppia*, *Zostera*, *Najas*, *Stratiotes*, and *Limncharis*. I propose, first of all, to describe my own observations, with the help of the figures, and afterwards to attempt certain general comparisons of the results obtained from those observations.

The materials used were the stems of representatives of the genera named shewing the points of origin of lateral roots. The material was stained, embedded, and cut in the microtome by the paraffin method in the usual way.

*Alisma*. Plate IX. Figs. 1 to 4.

A young root is shewn in longitudinal section in Fig. 1. The pterome cylinder is distinct, and has a single initial. The periblem and dermatogen form a single layer at the apex. The calyptrogen is at this stage only one cell in thickness.

An older stage is represented in Fig. 2. The pterome cylinder is now distinct, and is terminated by a single initial cell. The axial row of cells seen so clearly in most roots examined is not so distinct in *Alisma* as in many of the other genera. In transverse section of a root (Fig. 3) at much the same stage of growth as Fig. 2, a cell of the axial row is seen with one layer of pterome cells grouped round it, surrounded in turn by periblemic tissue. Returning to Fig. 2, the dermatogen has been split off from the periblem and is shewn as a single layer; both dermatogen and periblem, have, however, a common origin in the single initial cell. The cells of the cortex to the exterior show a width greater than those more internally placed. This is also seen in Fig. 3, which shews that since the same approximate number of cells are present in each concentric layer of the cortex, the cells in the external layers must widen in a tangential direction. The calyptrogen at the stage seen in Fig. 2, is four layered.

No longitudinal section was found shewing the embryogenic tissue fully differentiated into tissue elements. A transverse

section, however, is shewn in Fig. 4, taken at the stage when the development of the vascular elements has begun. The pericycle is seen as a distinct row enclosing five groups of fairly large cells about to become xylem elements, and five alternating groups of smaller cells, the initials of the phloem. In the centre is a large axial cell which will give rise to vascular elements.

Van Tieghem (2) (Plate XXXIII., Figs. 510 to 514) figures longitudinal sections of young lateral roots of *Alisma*. The chief points of difference between his figures and my own are that while the "digestive sac" is clearly indicated in Van Tieghem's drawing my preparations do not shew it. From Van Tieghem's figures one would imagine that the root-cap ("epidermis") and the "digestive sac" had the same origin. Moreover Van Tieghem evidently finds two initial cells in the plerome cylinder, whereas I could find only one in my preparations.

*Butomus umbellatus.* Figs. 5 and 6.

Fig. 5 represents a root at a fairly young stage. The plerome shews very clearly one large initial cell from which the remainder of the plerome is cut off, and distinct signs of a central axial row. Another large initial cell gives rise to the periblem and the dermatogen. The calyptrogen has divided at the apex to form a two-layered root-cap.

An older stage is seen at Fig. 6. The central axial row of the plerome is very distinct, being formed of large isodiametric cells which cut off no lateral segments. The pericycle in this case is evidently formed at the first division of the apical cell; the endodermis is not yet formed, and the root-cap is six layers in thickness.

Transverse sections, of which none are figured, shewed the same general characters as *Alisma*.

In Van Tieghem's (2) figures of the development of the root in *Butomus* (Plate XXXIV., Figs. 525 to 530), the same criticisms are applicable as have already been made with reference to *Alisma*.

*Vallisneria.* Figs. 7 to 9.

A young stage of a root in longitudinal section is shewn at Fig. 7. The plerome consists of a central row surrounded by a single layer of cells and arises from a single initial cell. The periblem and dermatogen also arise from a single initial cell, from which is cut off on either side a segment which remains undivided, the second lateral segment dividing parallel with the root surface to

form the dermatogen. An older stage is shewn at Fig. 8. The root-cap is four-layered, but a fifth layer may be noted towards the outside, which has a different appearance and has different staining properties to the others; this is probably the endodermis of the parent stem. The outermost layer of periblem cells is seen to have greatly increased in width, a circumstance noted in many of the plants examined.

A transverse section of the young root of about the same age as that shewn at Fig. 7 is given in Fig. 9. The central axial row of the plerome is surrounded by a single layer of pleromic cells. Lying to the outside of this and fitting in between the individual cells is the innermost layer of the periblem. Then come four other layers of periblem, concentrically arranged, each cell immediately behind the corresponding cell of the preceding row, and each row containing the same number of cells. Then follow the dermatogen and a one-layered root-cap.

*Ruppia.* Fig. 10.

A stage in the development of the root is figured (Fig. 10). The plerome cylinder has a single initial cell, and a prominent central axial row which cuts off no lateral segments. The pericycle has not as yet been differentiated. A single large initial cell gives rise to the periblem and the dermatogen. At this stage the root-cap is two-layered.

*Naias.* Fig. 11.

A longitudinal section of a young root is shewn at Fig. 11. The plerome cylinder appears to arise from two initial cells, though this point was not easy of determination. A single initial cell gives rise to the periblem and the dermatogen. The root-cap consists at this stage of two layers, the cells having a peculiar pentagonal shape not seen in any other genera examined.

*Zostera.* Figs. 12 and 13.

A young root is seen in longitudinal section at Fig. 12. The root-cap is two-layered. A single initial cell gives rise to the plerome cylinder, and a single initial cell, with an undivided segment on either side, to the periblem and the dermatogen.

Fig. 13 shews a young root in transverse section. The characters are those described for the preceding figures.

Van Tieghem does not figure the root apices of *Ruppia*, *Naias* or *Zostera*.

*Stratiotes.* Figs. 14 and 15.

A fairly advanced stage is shewn in longitudinal section at Fig.

14. The plerome cylinder originates by the division of a single initial cell. The pericycle is probably not cut off by the first division wall. There is present a central axial row, but this is not very clearly marked, and the cells are not longer than the remaining pleromic cells. In transverse section it is seen that the cells of the plerome are very irregular in shape and arrangement (Fig. 15), differing widely from the other genera examined. They are packed round the central cell in no particular order.

A small initial cell gives rise to the periblem and dermatogen, the layer forming the dermatogen dividing further away from the apex. The root-cap is massive, and the cells outwardly appear to lose their tabular form. Van Tieghem considers the outer layers of the root-cap to be formed by the divisions of the endodermis of the stem. In the material used, the endodermis of the stem, if present, could not be determined.

*Limnocharis.* Figs. 16 to 19.

A young stage is shewn at Fig. 16 in longitudinal section. The plerome cylinder arises from a single initial. A single initial with an undivided segment on either side also gives rise to the dermatogen and the periblem. The root-cap is two-layered.

An older root is shewn at Fig. 17. The central axial row is well seen, and the pericycle does not appear to be cut off by the first division plane of the single initial cell of the plerome. The root-cap is five-layered.

*Limnocharis* was the only genus examined in which the embryogenic tissue had become at all differentiated into tissue-elements, at any rate as seen in longitudinal section. Figs. 18 and 19 are longitudinal and transverse sections respectively of such a root. In Fig. 19 the root-cap cells are larger and their staining properties different to the other cells of the root. In the plerome cylinder the cells of the central axial row elongate further back from the apex, and become lignified. Other cells in the pleromic tissue also become lignified and shew spiral markings. In the transverse section this is also well seen. The xylem cells become lignified, from the pericycle inwards.

GENERAL COMPARISON OF RESULTS OBTAINED FROM THE  
INVESTIGATION OF YOUNG ADVENTITIOUS ROOTS OF THE  
GENERA OF MONOCOTYLEDONS NAMED.

I.—*The Origin from the Internal Tissues of the Stem.*

Van Tieghem (2) says that the root arises entirely from the pericycle of the stem, and that the arc of the endodermis external

to it develops a "digestive sac" of greater or less thickness, and that this envelopes the root up to the time of its exit. In the present investigation neither the origin from the pericyclic cells nor the endodermis forming a "digestive sac" were traced; moreover, the pericycle and the endodermis of the parent stem could not be distinguished as differentiated layers. One section figured, however, that of a fairly young root of *Vallisneria* (Fig. 8) shews what appears to be a layer outside those formed by the calyptrogen, which differs in size and colour and has no common origin with the outer layers of the root-cap. This, perhaps, arises from the endodermis of the stem. In *Vallisneria* the central tissue of the stem appears to be more clearly marked off from the cortex than in others examined.

Van Tieghem traces the roots from the division of two or three cells of the "rhizogenic arc" of the pericycle, which by one tangential division cut off the central cylinder and by a second tangential division exterior to the first cut off the cortex. The cells at the base of the cortex of the root are called by Van Tieghem the "epistele," and are formed, he considers, from the lateral cells of the "rhizogenic arc," and not from the central cell which cuts off the cells which become the initials of the plerome, the periblem and the root-cap, and so are not covered at the base, at any rate when older, by the root-cap or the dermatogen.

In the present investigations the junction of the base of the root with the stem was not clearly marked, but Van Tieghem's "epistele" was certainly not observed; the cells at the base of the cortex of the lateral roots appeared to merge into those of the cortex of the stem.

## II.—*Apical Meristem and the Initial Groups.*

In the plants examined three sets of initial cell-groups were distinguished, giving rise respectively to (1) the plerome, (2) the periblem and dermatogen together, (3) the calyptrogen. Now Janczewski (3), according to De Bary, finds in most of the roots of Monocotyledons these same three sets of initials, and among those plants he examined those also investigated in this paper, are *Alisma* and *Stratiotes*. Treub (4) (according to De Bary) for the most part confirms Janczewski, mentioning especially *Limncharis* and *Stratiotes*. In some plants, however, among them *Alisma* and *Butomus*, he says there is a common group of initial cells, two layers thick, from which the root-cap, the dermatogen and the periblem arise. This is contrary to the results obtained in the present investigation.

Van Tieghem (2) considers that all roots whether adventitious or not, whether of Monocotyledons or of Dicotyledons with very few exceptions have three sets of initials, giving rise to (i.) the plerome, (ii.) the periblem, (iii.) the many-layered epidermis acting as a root-cap. The plants of which he gives figures, and which I have also examined, are *Alisma*, *Butomus*, *Vallisneria* and *Stratiotes*.

According to my investigations the number of the initials for the different layers is usually as follows:—for the plerome one initial, for the periblem and the dermatogen a single common initial with occasionally an undivided segment on either side, though sometimes two initials appear to be present.

### III.—*The Plerome Cylinder.*

The plerome cylinder is surrounded by the pericycle. This layer is well-marked in all the plants examined and appears to be differentiated very near the apex, and is apparently often continued over the apex of the cylinder by the initial cell. The first cells cut off from the initial of the plerome on either side become the first pericyclic cells and remain undivided as a single layer, or rather cylinder, of cells surrounding the remaining pleromic tissues. Sometimes, as is seen in *Limncharis* (Fig. 18), the pericycle is not differentiated at the very apex, but the cells near the initial split behind to form part of the inner tissues of the cylinder. In this case the side segments of the initial cell form the whole of the pleromic tissues except the central single well-marked axial row which is formed by the posterior segments of the initial. When these segments form a strongly-marked central row they do not divide further, but the pleromic cylinder is completed, either by divisions of the primary lateral segments of the initial, into pericycle and inner tissue, or by the division of cells cut off at the same time as the pericycle (which then remains undivided) from the side of the initial. If the axial row be not so strongly marked it may cut off lateral segments to complete the cylinder, but it does not divide to form rows of cells itself. The root remains, in transverse section radially symmetrical, with a single central cell. The segments, in whatsoever manner they may be formed, divide as they grow older, this forming double rows, many of which divide again. These cells divide, however, in no predetermined order.

All the cells a short distance behind the apex are quadrilateral in longitudinal section. In transverse section they are seen to be arranged regularly in concentric rings around one central cell. The cells appear in transverse section to be five or six-sided, and

the cells in the next outermost ring alternate with those of the next projecting between those of the other layer as is shewn in *Zostera* (Fig. 13).

As it grows older the cells of the middle row become wide, thick-walled, and elongated, exhibiting the spiral markings characteristic of protoxylem. Other cells of a similar appearance, but of smaller size, are to be seen in the surrounding tissue in *Limnocharis* (Figs. 17, 19). Here the first cells to become lignified are those next the pericycle, and this lignification soon follows in the cells immediately inside. Small groups of phloem elements appear between the protoxylem groups. It may be noted that the xylem elements are developed centrifugally as Buscolione (5) and Pirotta (6) have already stated. It is true that the lignification may take place centripetally as is shewn in Fig. 19, but the actual formation of the elements takes place from the centre to the outside. Many of the figures in longitudinal section shew the central row of cells gradually elongating to form an axial vascular row. Fig 18 in particular shews that the lateral vascular elements being formed at a later stage.

#### IV.—*The Periblem and the Dermatogen.*

The common initial for the periblem and the dermatogen is usually situated just above that for the plerome. It may cut off a segment on either side which at first remains undivided, or this segment may at once divide tangentially, the interior cell seen in longitudinal section giving rise to a single external layer of cells, the dermatogen of which remains undivided, the posterior cells all dividing to complete the periblemic tissue. However three rows may be formed at once, as in *Butomus* (Fig. 6).

The dermatogen cells usually remain the same size, and are quadrangular (in longitudinal section), throughout the whole length of the root.

The cell giving rise to the periblemic tissue may divide transversely once or twice and become broader as it gets more room, as in *Limnocharis* (Fig. 17), or it may divide at once by a periclinal wall on the side away from the plerome. This first external segment of the cortex forms, usually by transverse divisions, a single layer of cells (*Limnocharis*, Fig. 17), the exodermis, or outside layer of the cortex. This layer is peculiar in that its cells widen very much as they recede from the apex, and at length may divide equally as in *Limnocharis* (Fig. 18). The cell from which this segment is cut proceeds on the same plan, and first



divide transversely once or twice and then cuts off one or two segments by periclinal walls. These segments may, by transverse divisions, form layers whose cells do not divide tangentially, or each layer may give rise to two or more layers, the outer layer usually consisting of smaller cells than the inner. Thus it is obvious that the endodermis cannot be differentiated at the apex as it is the innermost layer and the last to be cut off. All the cells of the periblem are quadrangular in both longitudinal and transverse sections. In transverse sections they shew a remarkably regular arrangement in concentric circles. The exodermis with its broad cells is clearly seen, widening in one direction only, that is, along the radius. Transverse sections also shew that as the cells towards the exterior grow longer, they divide in a radial direction; in such sections the cells of the endodermis appear to be five-sided. The cells of the endodermal layer form a ring immediately outside the ring formed by the cells of the pericycle; but an individual cell of the endodermis does not lie immediately outside an individual cell of the pericycle, but the apex of its pentagon fits in between two cells of the pericycle. This is clearly seen in the illustration of *Alisma* (Fig. 3).

#### V.—*The Root-cap.*

The root-cap arises from the single layer of cells known as the calyptragen, which covers the apex of the root. Each cell of this single layer may divide anticlinally, thus increasing the number of cells in this single layer. All the cells except those furthest from the apex may also divide periclinally. As the result of this, the original single layer becomes double, except in regions furthest from the root apex where it remains as a single layer. The next periclinal walls are formed in the innermost row of the double-layered root-cap. These walls are formed in all the cells save those furthest from the root apex. Thus at the apex the root is covered by a three-layered cap, a short distance from the apex this becomes two-layered and further away still the root-cap consists of a single layer only. The subsequent divisions in the cells of the root-cap take place on a similar plan, that is, periclinal walls are continually being formed in the median cells of the innermost layer of the root-cap, so that after several layers have been thus formed very few cells are concerned in the process. Although this is the ground plan periclinal walls may also be formed at the same time in other outer layers of the root-cap; no walls, save anticlinal ones, are, however, formed except in the innermost layers. Anticlinal divisions

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are necessary to enable the outer layers to expand sufficiently to enclose the increased number of inner layers.

My results appear to support the views held by De Bary, inasmuch as they seem to shew that the roots of the aquatic Monocotyledons studied are developed in the same way as are, according to De Bary, the majority of the roots in that group, that is, from three sets of initials giving rise respectively to (i.) the calyptrogen, (ii.) the periblem and dermatogen together, (iii.) the plerome.

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10. Flahault. Ann. Sci. Nat. ser. 6, tom II.
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### DESCRIPTION OF FIGURES ON PLATE IX.

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|----------|---------------------|---|
| Fig. 1.  | <i>Alisma.</i>      | A longitudinal section through the apex of a young root.            |
| Fig. 2.  | <i>Alisma.</i>      | A longitudinal section through the apex of an older root.           |
| Fig. 3.  | <i>Alisma.</i>      | A transverse section through a root at some distance from the apex. |
| Fig. 4.  | <i>Alisma.</i>      | A transverse section through a fairly old root.                     |
| Fig. 5.  | <i>Butomus.</i>     | A longitudinal section through the apex of a young root.            |
| Fig. 6.  | <i>Butomus.</i>     | A longitudinal section through a somewhat older root.               |
| Fig. 7.  | <i>Vallisneria.</i> | A longitudinal section through a young root.                        |
| Fig. 8.  | <i>Vallisneria.</i> | A longitudinal section through an older root.                       |
| Fig. 9.  | <i>Vallisneria.</i> | A transverse section through a root a short distance from the apex. |
| Fig. 10. | <i>Ruppia.</i>      | A longitudinal section through a young root.                        |
| Fig. 11. | <i>Najas.</i>       | A longitudinal section through a young root.                        |
| Fig. 12. | <i>Zostera.</i>     | A longitudinal section through the apex.                            |
| Fig. 13. | <i>Zostera.</i>     | A transverse section through the root near the apex.                |
| Fig. 14. | <i>Stratiotes.</i>  | A longitudinal section through the apex of a root.                  |

- Fig. 15. *Stratiotes*. A transverse section through the root near the apex.  
Fig. 16. *Limnocharis*. A longitudinal section through a young root.  
Fig. 17. *Limnocharis*. A longitudinal section through a somewhat older root.  
Fig. 18. *Limnocharis*. A longitudinal section through a fairly old root.  
Fig. 19. *Limnocharis*. A transverse section through a root some distance from the apex.

EXPLANATION OF THE LETTERING.

*pl.*, plerome. *pb.*, periblem. *cal.*, root-cap. *ed.*, endodermis. *pr.*, pericycle.  
*d.*, dermatogen. *ct.*, cortex.

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NOTES FROM THE CAMBRIDGE BOTANY SCHOOL.

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II.—TRACHEIDS IN THE NODAL REGION OF  
*EQUISETUM MAXIMUM*.

By M. G. SYKES,  
Girton College, Cambridge.  
[TEXT-FIG 26, 1—5.]

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WHEN cutting transverse sections through a node of *Equisetum maximum* in order to observe the indications of secondary thickening noted by Cormac,<sup>1</sup> some very curious large reticulately pitted tracheids were observed in the lumen of a earinal canal just below the nodal region.

Cormac pointed out that, in view of Strasburger's<sup>2</sup> statement that water is conveyed through the lumen of the earinal canals, and as these canals are not continuous from one internode to the next, some elements must be provided to convey the water from one canal to another at the node. He suggested that the explanation of the proliferation of tracheids at the node (by secondary thickening), might lie in the necessity for such provision.

It seems probable that the peculiarly large elements shown in the accompanying figures may have some special connection with the transport of water between the canals of adjacent internodes.

In transverse sections, a little distance above the node a few reticulately pitted elements are seen on either side of the vascular bundle; as the sections approach the node these elements increase in number and size and begin to project into the earinal canal (Text-Fig. 26, 1 and 2). The canal is soon filled up by them; at the point of entrance of the leaf-trace, which is also the region of forking

<sup>1</sup> Cormac. *Annals of Botany*, Vol. VII., 1893, p. 63.

<sup>2</sup> Strasburger, *Leitungsbahnen*, pp. 435-438.

of the bundle, a very considerable amount of xylem is present. Just below this point a space begins again to be visible, and those of the xylem elements which project into this space are of enormous size and of marked peculiarity (Text-Fig. 26, 1, 2, 4). In two cases (3 and 5) a single large tracheid was found entirely filling up the space. Sections below this region show that the space is the top of the carinal canal of the next internode and a gradual transition to the normal internodal structure now occurs.

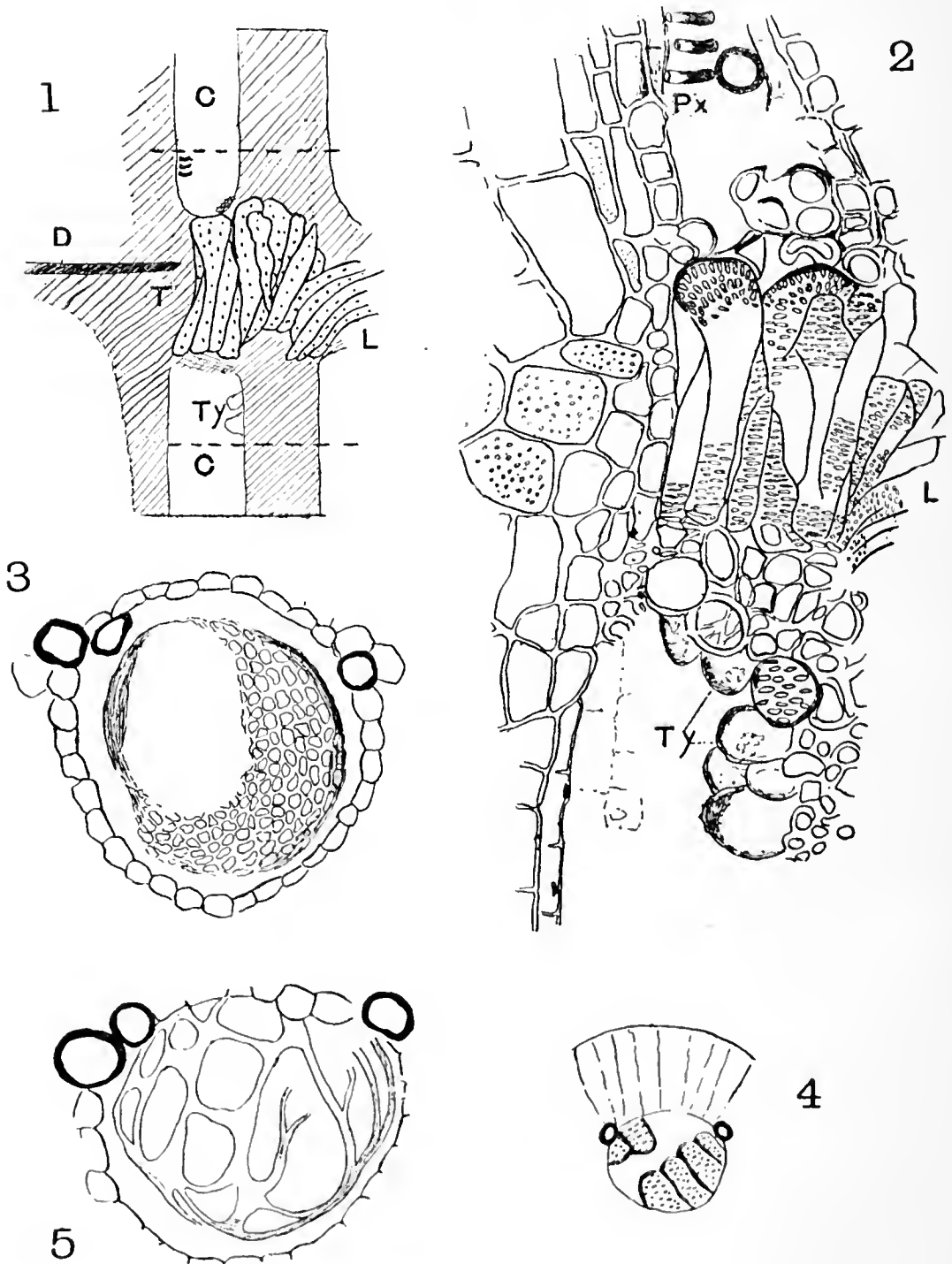


Fig. 26.

1. Diagram of longitudinal section through node of *Equisetum maximum*. *D*, diaphragm of thick-walled cells; *C*, carinal canals above and below node; *T*, tracheids at node, some passing out as leaf-trace. (*L*).
2. Part of the same section (enclosed between the broken lines in Fig. 1); shewing a large number of reticulate tracheids at the node bulging out above into the canal and passing below the node into large broken rings of lignified tissue. *Ty.*, tyloses from cortical cells below node; *Px.*, rings of protoxylem.
3. Transverse section through a carinal canal just below a node of *E. maximum*, shewing a single large reticulate element nearly filling up the lumen. Three xylem tracheids are seen at the edge of the canal.
4. Transverse section below the node, shewing several reticulate elements projecting into the lumen of the carinal canal.
5. Transverse section shewing a large meshed reticulum in the lumen of a carinal canal just above the node.

Longitudinal sections were cut through the node, and, in one of these, two carinal canals, one above and the other below the node, happened to be cut (1 and 2). Into the lumina of these canals the large reticulate elements, which had before been seen in transverse section, projected, nearly filling up the ends of the canals. A considerable number of small reticulate elements, noted by Cormac, were seen to connect the larger elements. In the same section several tyloses were formed by the vascular parenchyma, and projected into the lumen of the lower canal.<sup>1</sup>

In order to determine whether the large reticulately pitted tracheids were used in conduction, a branch of *Equisetum maximum* was fastened to a vacuum pump, and one end was dipped into a watery solution of eosin. After two hours the solution had reached the top of the branch and sections were then cut in order to examine the regions stained. In the internodes the walls of the canals were very deeply stained, but towards the nodes, (*i.e.* as the reticulately pitted elements appeared and increased in number), their stain became very slight, while the reticulate elements all took the stain. The larger tracheids projecting into the top and bottom of the canal were also stained, but not quite so brightly as the smaller tracheids.

The large xylem elements are of such remarkable character that it is natural to regard them as serving some special purpose. Their position, in the extreme ends of the canal lumina, certainly suggests them to be of importance in the conduction of water from canal to canal by means of the small reticulate tracheids. In longitudinal section it is seen that they are continuous with the small tracheids, and some of them, at any rate, must be looked upon as greatly enlarged extensions of these.<sup>2</sup>

<sup>1</sup> Strasburger, *loc. cit.*, p. 437.

<sup>2</sup> cf. Williamson. *Phil. Trans. R. Soc.*, 1871. Pl. 28, Fig. 40.

Another explanation as to their function might be that they are water-storing elements, but this does not seem probable in a plant of the habit of *Equisetum*. The eosin experiment also showed that they were used in conduction.

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## NOTES ON RECENT PHYSIOLOGICAL LITERATURE.

### I.—THE CHEMISTRY OF PHOTO-SYNTHESIS.

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- H. Euler. Zur Kenntniss der Assimilationsvorgänge I., Ber. d. deut. chem. Gesell. XXXVII., p. 3411, 1904.
- F. Usher and J. Priestley. A study of the mechanism of Carbon Assimilation in Green Plants. Proc. Roy. Soc., B Vol. 77, p. 369, Jan. 1906.
- R. Meldola. The Living Organism as a Chemical Agency: a Review of Some of the Problems of Photo-synthesis by Growing Plants. Presidential Address to the Chemical Society, Jour. of Chem. Soc., April, 1906.
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THE object of this short notice is to direct the attention of readers to recent papers on the chemical mechanism of  $\text{CO}_2$ -assimilation. The early view which regarded protoplasm as an enormous molecule which, in assimilation, took up  $\text{CO}_2$  directly, on the one hand and split off sugar on the other hand, has given place to the newer view, so much more hopeful for investigation, which holds that, in such functions as respiration and assimilation, we have to deal with a system of comparatively simple changes occurring in sequence, and that if we are only clever enough we shall be able to separate these stages.

Von Baeyer in 1870 first suggested that production of formaldehyde was an important stage in photo-synthesis, forming a sort of turning point between the reduction-processes that formed it from aqueous carbonic acid and the "condensation"-processes that caused it to be built up into sugar and starch.

In 1877 Erlenmeyer indicated that formic acid would probably be the intermediate stage in the reduction-process.

Since that time a number of isolated experiments have been made on the reduction of  $\text{CO}_2$  by light, *in vitro* as well as in the plant, but systematic critical investigation has only been taken up in the last two or three years. Investigation has been directed to four points. (i.) Does formaldehyde really occur free in the green assimilating leaf? (ii.) Can  $\text{CO}_2$  be reduced by light *in vitro* in any way that will help to elucidate the process in the cell? (iii.)

What is the fate of the oxygen separated from the carbon in the reduction-process? (iv.) Is the reduction-process in the cell, wholly or partly, a non-vital change?

In 1904 H. Euler published the first paper of the new era in which he proposed to begin his systematic study of the assimilation-process by critically repeating and extending the scattered observations of others.

He reinvestigated the question of the presence of free formaldehyde in assimilation. Polacci had shown that the distillate from an extract of assimilating leaves gave a turbidity with anilin due to the formation of methylen-anilin.<sup>1</sup>

Euler finds that the extract itself gives very much less reaction than the distillate and that an extract of dried hay gives also the same reaction. Conclusions as to the presence of free formaldehyde in leaves must therefore be drawn only with great caution. Euler next repeated the experiments of Bach who had announced that he had found  $\text{CO}_2$  reduced to formaldehyde by the action of uranium acetate, as an optical sensitiser, in sunlight. This seemed to provide an inorganic parallel with the action of chlorophyll in the living leaf. By doing more careful control experiments than Bach, Euler seems to have proved that the same reduction-process takes place—though more slowly—in the light, *without*  $\text{CO}_2$ . The action of the current of  $\text{CO}_2$  passed through the solution of uranium acetate seems to have been in removing the oxygen present; nitrogen or hydrogen is said to act equally well.

Bach had also asserted reduction of  $\text{CO}_2$  to formaldehyde by dimethyl aniline in sunlight, or even in the light of a gas-flame. Euler appears to show conclusively that this effect is due to impurities in the dimethyl aniline.

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In January of this year Usher and Priestley published a striking paper on this question. Their first point is a confirmation of the reduction of  $\text{CO}_2$  by Uranium Salts in sunlight, asserted by Bach. By using highly concentrated  $\text{CO}_2$  in a sealed tube they get very abundant reduction to formic acid.

With regard to this result, the reader is very much perplexed by the fact that these authors simply do not mention Euler's work or his criticism of Bach's conclusions. Until these divergent opinions have been clearly harmonised a certain suspension of

<sup>1</sup> This is an extremely delicate test for formaldehyde (possibly dangerously delicate in view of the assertion that traces of formaldehyde always occur in the atmosphere). One part of it in 20,000 of water can be detected.

judgment is inevitable. The great pitfall of this class of work seems to be the neglect to do elaborate and thorough control experiments so that every imaginable cause except the alleged one is excluded, and we hope these authors will not rest satisfied with their excellent start, but will thresh out the whole matter.

Turning to the state of affairs in the green cell, Usher and Priestley are able to put forward a complete scheme of the stages of the reduction of  $\text{CO}_2$ . The form of this is simple and reasonable and is supported by some experimental evidence at each step. If further experiments render this interesting scheme proof against all attack, it will be a very noteworthy advance in the chemical analysis of those processes which were formerly lumped together as "protoplasmic."

Three separable stages in photo-synthesis are suggested. (a)  $\text{CO}_2 + \text{Water}$  is converted to formaldehyde + hydrogen peroxide, the chlorophyll acting as an optical sensitiser; this stage is held not to involve the vitality of the cell. (b) The formaldehyde is removed and condensed to a sugar by the action of the protoplasm. (c) The hydrogen peroxide is removed by being split up by an enzyme to water and oxygen, the latter being set free in the gaseous form.

The experimental evidence, chiefly from *Elodea*, put forward on the various stages may be briefly indicated. Formaldehyde actually is formed in green cells, as various tests show. It can best be demonstrated when the protoplasm has been killed, as then it is not removed and condensed. In boiled leaves, lacking both enzyme and protoplasm, the hydrogen peroxide also accumulates and soon bleaches the chlorophyll. In chloroformed leaves, the enzyme remains and at first splits up the hydrogen peroxide, but after a time the accumulating formaldehyde "poisons" the enzyme and stage (c) also ceases. If *Elodea* leaves be put in solution of hydrogen peroxide the green cells decompose it freely and bubbles of oxygen arise.

In a second quite recent communication,<sup>1</sup> Usher and Priestley state (i.) that a very thin film of concentrated chlorophyll will by itself decompose  $\text{CO}_2$  in sunlight, (ii.) that if this film be superposed on a film of gelatine containing the right enzyme, oxygen is evolved from the  $\text{CO}_2$  and the formation of formaldehyde is demonstrable. Thus the whole reduction-process is non-vital and the protoplasm only comes in to condense the formaldehyde to sugar.

There is one rather important general consideration which seems to the writer to be opposed to the view that the formation of formaldehyde in the cell is outside the activity of the protoplasm.

<sup>1</sup> Communication to the Royal Society, May 10th, 1906.



By various causes, as by drugs, senility, accumulation of the products of assimilation, etc., the power of assimilating can be much reduced below the normal. Now these causes affect the protoplasm rather than the chlorophyll, and it would be expected that the first, non-vital, stage would be unimpaired by them. Formaldehyde should then accumulate faster than the protoplasm could deal with it and poisoning should result; which however does not happen. If formaldehyde can be accumulated, without reversion, in some form, setting in, so as to "poison" the enzyme of a chloroformed cell; *à fortiori* it can accumulate so as to poison the protoplasm of a cell which is only condensing it at a sluggish rate.

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The researches that we have been considering are also dealt with by Meldola in the first part of his lucid and useful Presidential Address to the Chemical Society. Reference will be found there to a quantity of literature dealing with the purely chemical side of this important question.

The greater part of this Address is, however, devoted to the chemistry of the condensation of formaldehyde to sugar, a field in which, thanks to the researches of Emil Fischer, the chemist is well ahead of the biologist and can give him valuable indications. Among many other significant pieces of knowledge it is pointed out that we now know that such a gentle catalytic agent as Calcium carbonate can start the condensation of formaldehyde, so that we come near to such agents as may be found in the living cell.

Meldola urges the general view that a number of different organic substances, and not sugars only, may possibly arise as the result of photo-synthesis in the green cell.

F. F. B.

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## BOTANY AT THE FORTHCOMING MEETING OF THE BRITISH ASSOCIATION.

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THE meetings of Section K at York from Thursday, August 2nd to Tuesday, August 7th, under the Presidency of Professor F. W. Oliver, F.R.S., will be organised on the lines that have become usual during the last few years. At least three of the Sessions of the Section will be devoted to special topics of current interest, the proceedings in each opening with a general paper or address dealing with the topic as a whole, followed by more special

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papers and a general discussion. In this way the interest of members is focussed on one general topic throughout a Session, instead of being distracted by a succession of miscellaneous papers.

The three topics chosen for the present meeting may be described in a general way as follows:—

“Some Aspects of the Present Position of Palæozoic Botany” will be dealt with by Dr. D. H. Scott, F.R.S., and “The Conditions of Growth of Carboniferous Plants” by Professor F. E. Weiss, Miss M. C. Stopes and others. Various geologists specially conversant with the mode of occurrence of Carboniferous Plants have been invited to contribute to the discussion. This subject will occupy the Friday morning session.

“The Nature of Fertilisation” and kindred problems will engage the attention of the Section on Monday morning (August 6th). This will be a joint Session with Section D (Zoology). Mr. V. H. Blackman will open the proceedings with a general address setting forth the present position of the subject. Professor Farmer, F.R.S., is expected to contribute a paper on the cytological features of Apospory, and Mr. Doncaster one on Some Cytological Features of Animal Parthenogenesis. Several eminent foreign botanists, distinguished for their work on kindred topics, who will be in England attending the Conference on Plant-hybridism to be held in London immediately before the meeting of the Association, have promised to be present. Among these are Professor Tschermak of Vienna, Professor Johansen and Dr. Ostenfeld of Copenhagen, Dr. Rosenberg of Stockholm and Dr. Lotsy of Leiden.

“The Phylogenetic Value of the Vascular System of Seedlings” will occupy the Section on Tuesday morning (August 7th). Mr. A. G. Tansley and Miss E. N. Thomas will open the proceedings, while Professor Jeffrey of Harvard, Messrs. A. W. Hill, T. G. Hill, and Miss Ethel Sargent are expected to contribute by papers or otherwise to the discussion.

While it is thought very desirable to make the type of Session described the backbone of the meeting of the Section, it is quite undesirable, and not in accordance with the aims of the Association, to exclude miscellaneous papers of interest and importance from attention. Accordingly several Sessions have been left open for these. Where possible they will be grouped under different headings and the whole or part of a Session devoted to each group.

Thursday afternoon (August 2nd) will thus be devoted to papers

on Vegetation Survey, Mapping, and Ecology. Dr. T.W. Woodhead, who has been spending the last year at Zurich with Professor Schröter, will communicate a paper on "Ecological Work in Switzerland," Mr. C. E. Moss will give an account of Survey Work and Mapping in Somersetshire, while Dr. Fritsch and Mr. Walker will contribute papers on Algal Ecology.

Professor Wyndham Dunstan, F.R.S. is expected to give a general account of his work on hydrocyanic acid in metabolism, but it is not yet certain whether this will be presented to the Botanical or to the Chemical Section. Among other papers may be mentioned Professor H. H. W. Pearson's on the Habitats and Habits of S. African Cycads, communicated by Mr. A. C. Seward, F.R.S. and Mr. Hugh Richardson's on the Vegetation of Teneriffe.

It is hoped that Dr. Blakeslee may be able to be present and give an account of his work on sexual differentiation in the Mucorineæ and also of his important recent discoveries of sexual differentiation in the spores of *Marchantia*.

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## SOME BOTANICAL EXHIBITS AT THE ROYAL SOCIETY CONVERSAZIONE.

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### FOSSIL PLANTS FROM THE ENGLISH COAL MEASURES.

THIS was a collective exhibit of petrifications from the well-known localities in Lancashire and Yorkshire, and it included important and novel contributions from a large number of those who are at present directing their attention to the field of Palæobotany.

DR. D. H. SCOTT sent specimens of the remarkable new stem which he has named *Sutcliffia insignis*—in honour of Mr. W. H. Sutcliffe, who has re-opened a disused coal-mine at Shore, Littleborough for the purposes of Palæobotany, and upon whose property the specimen was found. The stem is a large one with solid central cylinders giving off a number of subsidiary steles from which the numerous bundles supplying the leaves arise. The leaf-bundles are so closely similar to those of Seward's *Rachiopteris Williamsoni* that there can be little doubt that the latter must belong to another species of the same genus. The stem represents a new type of Medullosean structure which will be fully described in a forthcoming memoir now printing for the Linnean Society.

Those who have perused our report of the recent discussion on "The Origin of Gymnosperms" will have realised that a large number of supposed ferns of Palæozoic times are now recognized as seed-bearing plants. If there be any who still suppose that there were no real ferns in the flora of that epoch, Dr. Scott's beautiful sections of fossil fern-sporangia with the spores germinating *in situ* would have convinced them of the contrary. An account of these germinating spores was given in this Journal<sup>1</sup> some time ago, and it will be remembered that this paper was shortly followed by another in which certain sporangia were referred to *Stauropteris oldhamia*.<sup>2</sup> Evidence has since come to light shewing that the germinating spores of the former paper are referable to a species of *Stauropteris*; hence this genus belongs to the true ferns rather than to the Pteridosperms. It will be remembered that at the time the *Stauropteris*-paper was written<sup>3</sup> its systematic position was perfectly open.

In conjunction with MISS BENSON, DR. SCOTT shewed a number of excellent sections of the seed-like fructification of the little-known *Miadesunia membranacea*.<sup>4</sup> This little Lycopod, whilst recalling *Isoëtes* in some respects, agrees with *Lepidocarpon* in the seed-like peculiarity of its integumented megasporangium.

PROFESSOR F. W. OLIVER and MISS W. BRENCHLEY were responsible for models and preparations shewing new features in the structure of *Lyginodendron Oldhamium*. The models were built up section by section, and the result was a faithful reconstruction of two branching specimens exactly as they lay in the petrified nodule. Of the two stems which Miss Brenchley had modelled one bore numerous branches of the first degree whilst the other was characterised by a repeated branching which reached the third degree. In both cases all the branches arise in the leaf-axils, a feature in which the plant agrees with *Poroxyloa* (specimens of which were shown by Dr. Scott) and also no doubt with recent Cycads.

Among the other specimens shewn may be mentioned a ribbed *Sigillaria* of *Rhytidolepis*-type (by MR. ARBER), of interest in that it combined internal structure with surface characters; also a pretty rachis of a young *Zygopteris corrugata*<sup>5</sup> literally smothered in sessile

<sup>1</sup> Vol. III., p. 18, Jan. 1904.

<sup>2</sup> D. H. Scott. NEW PHYTOLOGIST, Vol. IV., p. 114.

<sup>3</sup> Loc. cit, p. 119.

<sup>4</sup> M. Benson, NEW PHYTOLOGIST, Vol. I., p. 58.

<sup>5</sup> Cf. F. E. Weiss. NEW PHYTOLOGIST, Vol. V., p. 82.

ramentum-like appendages. It will be remembered that *Botryopteris forensis* of the French Permo-carboniferous is also characterised by an abundance of somewhat similar dermal appendages.

COLONISATION BY BLUE-GREEN ALGÆ IN THE TROPICS.

DR. FRITSCH had arranged a small exhibit illustrating the colonisation of bare surfaces by sub-aerial Algæ (Cyanophycæ) in the Tropics. In the moist lowlands of Ceylon most objects tend to be clothed with a dense growth of this group of Algæ, and similar features are to be observed in any moist hothouse kept at a high temperature (e.g., the *Nepenthes* or Aroid houses at Kew). A series of rocks, and photographs of rocks, from the *Nepenthes*-house were shown in illustration of progressive stages in colonisation; and the exhibit was also illustrated by a few specimens from Ceylon and by microscopic preparations. The first blue-green forms to obtain a foothold are such as grow firmly attached to the substratum; according to the amount of rainfall and the temperature, this growth is either more or less dry and encrusting, or slimy and more or less gelatinous. Such adhesive growth gradually forms a compact investment, which prepares the way for algal forms exhibiting a higher type of growth; adhesive growth rarely attains any great thickness, probably owing to the difficulties of respiration within the mass. Tangled growth, which generally colonises the surface of the adhesive forms at an early stage, is much more suitable from the respiratory point of view, and may form a thick stratum, serving as a basis for the growth of vegetation of a higher type (e.g., small Bryophytes or Ferns). Wherever there is plenty of moisture in the air, however, the filaments of a tangle tend to grow out vertically from the substratum and to give rise to a kind of tufted growth; this is probably a response to a hydrotropic stimulus. Where such tufted growth is overshadowed it often assumes a well-marked stratified arrangement, often well seen on tree-trunks in the Tropics. When tangled or tufted growth first becomes colonised by small Bryophytes there is often keen competition between the two; the Alga twines round the Bryophyte, thus raising its filaments into the air, whilst the latter grows on in front so as to escape the invading Alga. In this way a thick carpet of algal growth is gradually formed. The wealth of vegetation on every conceivable object in the moist Tropics is primarily due to the agency of the Cyanophycæ.

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UNIVERSITY OF LONDON ADVANCED LECTURES  
IN BOTANY.

REFERENCE to the lectures organised by the Board of Studies in Botany has often been made in these pages.

With the Session just concluded the three years' course originally planned by the Board, but necessarily modified to some extent by various exigencies, has come to an end, and it may be of interest to record the courses that have been given.

## SESSION 1903—4.

Mr. A. D. Hall. "The Plant in Relation to the Soil in which it Grows." (Chelsea Physic Garden).

Dr. D. H. Scott, F.R.S. "The Lycopsidea." (University College).

Professor J. Reynolds Green, F.R.S. "Plant-Metabolism." (Chelsea Physic Garden).

## SESSION 1904—5.

Sir W. T. Thiselton Dyer, F.R.S. "Problems of Modern Botany." (Chelsea Physic Garden).

Mr. W. G. Freeman. "Current Work in Economic Botany." (Chelsea Physic Garden).

Mr. V. H. Blackman. "The Ascomycetes, especially in Relation to the typical fructification." (University College).

Dr. F. F. Blackman. "The CO<sub>2</sub>-economy of Plants." (University College).

Dr. A. B. Rendle. "The Tubifloræ." (Chelsea Physic Garden).

## SESSION 1905—6.

Mr. W. Bateson, F.R.S. "The Facts of Heredity." (University College).

Professor F. W. Oliver, F.R.S. "The Origin of Gymnosperms." (University College).

Professor J. B. Farmer, F.R.S. "The Bryophyta." (Chelsea Physic Garden).

When it is considered that practically all these courses have been largely based on the researches of the lecturers it will be admitted that their extraordinarily wide range speaks highly for the width and vitality of botanical investigation in England. London botanists highly appreciate the kindness and the trouble taken by the two lecturers from Cambridge, Mr. Bateson and Dr. Blackman,

<sup>1</sup> The substance of these lectures has been appearing in the pages of this Journal.

who readily responded to the invitation of the Board and contributed two of the most valuable courses.

The Board will in future arrange sets of courses from Session to Session.

The lecturers for 1906—7 will be as follows:—

Mr. Francis Darwin, F.R.S. "The Irritability of Plants."

Mr. A. G. Tansley. "The Evolution of the Vascular System in the Fern-Phylum."

Miss Ethel Sargent. "The Origin of Angiosperms."

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### THE ORIGIN OF GYMNOSPERMS AT THE LINNEAN SOCIETY.

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THE adjourned discussion on this subject (see NEW PHYTOLOGIST, Vol. V., p. 68) was resumed at the Meeting on May 3rd. The President first called on Dr. Scott, the last of the four "openers," to address the Meeting.

DR. SCOTT, rising at 8.15, said he would first like to make clear exactly what had been in the minds of those who had taken the view that the Cycads and probably the other Gymnosperms arose from a fern-like ancestry. In some quarters, though not among the previous speakers, the idea had gained ground that the view in question supposed the Cycads and their allies to have originated from some group represented among living ferns. But in 1895 he had suggested that *Lyginodendron* and *Heterangium* were derived from an ancestor belonging to a generalised or rather non-specialised fern-stock, and a few years later he had put forward the view that the common ancestors of Cycads and Cycadofilices were to be sought among simple ferns or fern-like plants. At no time had it been held that the Cycadofilices (or Pteridosperms) sprang from any family now known, still less from any recent family of ferns. As regarded the evidence for the origin of these groups there had been singularly little advance during the last few years. The whole *raison d'être* of this discussion lay of course in the recent discovery of seeds borne upon fern-like plants. Before these discoveries the only evidence available was that of the vegetative organs and particularly of their anatomy, which had led to the conclusions indicated. Then, about three years ago, had come the discovery that one of these fern-like plants bore seeds, and that was quickly followed by other similar discoveries. As a matter of fact these discoveries of seeds scarcely touched the problem of the origin of the group, because the seeds in question were good, typical, well developed seeds, on a level with those of Cycads and much too advanced to throw light on the origin of the organ. So the question of the derivation of these plants remained in very nearly—though not quite—the same condition as before these recent discoveries. With regard to the anatomical characters they indicated a clear affinity with the Ferns rather than with any other group of Pteridophytes. He would shew them a lantern slide of a transverse section of a very young stem of *Lyginodendron oldhamium*—one of the most completely known of fossil plants, since we knew its stem,

roots, leaves, and its male and female reproductive organs—and would point out its strong similarity with that of *Osmunda*. He would also illustrate the similarity of its petiolar strand with that of *Lygodium*, not because he suggested any special affinity between *Lyginodendron* and these ferns, but to exhibit the undoubted Filicinean affinities of the genus. The anatomical characters also suggested Cycadean affinities, and on this point the discovery of the seed was quite decisive. The male organs, which we were now beginning to know, further supported the Filicinean affinities of *Lyginodendron*. Mr. Kidston had described *Crossothea Hæninghausi*, of which he would shew them a lantern slide, and had proved that the sterile leaflets connected with it were identical with *Sphenopteris Hæninghausi*, known as the leaf of *Lyginodendron*. Some years ago Miss Benson had described a fructification shewing structure as the microsporangia of *Lyginodendron* and had called it *Telangium*

**8.30** *Scotti* (lantern slide). This was probably identical, or at least co-generic, with *Crossothea Hæninghausi*. These sporangia were united into synangia. There was a fossil named *Scolecopteris* (lantern slide) which shewed synangia and had always been considered Marattiaceous, but it was so much like *Crossothea* that just possibly it and others of the same type also might be the male fructification of a Pteridosperm. He would shew them illustrations of the synangia of various Marattiaceæ, and point out that the male organs of Pteridosperms were really so much like them that we might fairly conclude their common ancestors to have been fern-like. Lately things had gone rather further than they had anticipated. The actual number of known "seed-bearing Ferns" was not great, some half-dozen in all, but they represented nearly every group of carboniferous Ferns, so that suspicion was cast upon the whole. It was the distinguished French palæo-botanist, Professor Zeiller, who first made the difficulty acute. At one time he was rather sceptical on the subject of the Cycadofilices, inclining to regard them merely as a peculiar group of ferns, but the recent discoveries had made him an ardent convert, and recently he had published an article in the "Revue Générale des Sciences" in which he showed how the position had changed. If, he asked, these supposed Ferns were all, or nearly all, Pteridosperms, where were the Ferns from which they came? Now it was true that Ferns could not be regarded as the dominant group in the Palæozoic they were once thought, but the chances were that the Botryopteridæ and some of the plants with fructifications of the Marattiaceous type were genuine Ferns. The Botryopteridæ were certainly a fairly varied group, though they were not much known except to the specialist. One thing we must always remember about the Carboniferous flora. We were attempting to reconstruct the whole flora from an extremely fragmentary portion of it to which alone we had access. It was like trying to reconstruct the present flora of England from the plants found on Walberswick Marshes. There was one point in Professor Oliver's opening address he could not agree with. He was very glad to see a reaction against the view that there were no Palæozoic Ferns, but he thought Professor Oliver went too far in suggesting that there might have been true cryptogamic Cycadofilices, e.g., a cryptogamic *Lyginodendron*, mixed with the Pteridospermic members. Professor Oliver had cited the Palæozoic Lycopods, some of which had seed-like organs while others were



purely cryptogamic. We had to remember that the anatomy of the seed-bearing *Lepidodendreae* was exactly like that of the cryptogamic forms, whereas it was the peculiar anatomy of the seed-bearing *Pteridosperms* that first suggested that they were not typical *Filicineae*. Further the seed-like organs of carboniferous *Lycopods* were clearly derived immediately from cryptogamic sporangia, while the seeds of *Pteridospermeae* were far removed from anything of the kind. As regarded the other great question under discussion, the origin of the *Coniferae*, the data were still very inadequate. The fossil *Coniferae* were very abundant and extremely unsatisfactory. Palaeobotanists were, in fact, without adequate knowledge of the structure of the earlier *Coniferae*, upon which the question must depend. The view that the *Coniferae* or, at least, the *Araucarieae* had descended from *Lycopods* was brilliantly stated by Mr. Seward at the previous Meeting. It was difficult to follow Mr. Seward if one did not quite agree with him. A fundamental point was the existence of the *Cordaiteae*, a synthetic carboniferous group. The structure of the stem and root was *Coniferous* and resembled that of the *Araucarieae*, while the leaves were *Cycadean*, and the male and female fructifications to some extent resembled those of *Ginkgo*, as he would shew by reference to diagrams. As Mr. Seward admitted, there was a series of forms which, anatomically speaking, connected the *Cordaiteae* with the *Pteridosperms*. Thus the *Cordaiteae* possessed characters pointing in no less than four directions. The structure of the wood, which he would illustrate, was admittedly indistinguishable from that of the *Araucarian Conifers*. This was of some importance because it was of the type characterising the *Conifers*, *Cordaiteae*, *Pteridosperms* and *Botryopterideae*. It was the great characteristic type of the Fern series throughout the Palaeozoic. *Lycopod* wood on the other hand was scalariform. This fact tended in the strongest possible degree to ally the *Cordaiteae* with the Ferns and to separate them from the *Lycopods*. Mr. Seward had not made his position quite clear. Did he really mean to sweep all the *Coniferae* into his *Lycopod* net? If so Mr. Seward was, he thought, in a position of considerable difficulty, because he would have to include the *Taxaceae* and *Ginkgo*. *Ginkgo* was universally admitted to have a *Cycadean* and therefore a *Filicinean* affinity, and it also had a real affinity with the *Taxaceae*, for instance with *Cephalotaxus*, established before the multiciliate spermatozoids were discovered. Was this to be disregarded? On the other hand, if the argument were intended to apply to the *Araucarieae* alone, where were we going to draw the line between *Lycopodinean* and *Filicinean Conifers*? Most botanists were agreed that the *Conifers* were a natural group, and it was a great deal to demand that they should be split up. Much had been made of the peculiarities of the *Araucarieae*, but it would be very difficult to maintain that they had no affinity with the *Abietineae*, for instance, or with the *Podocarpeae*. He must not keep them too long, but there was one point Mr. Seward had mentioned to which he must refer. He did not dispute the great geological age of the *Araucarieae*, nor their relatively primitive position, in relation to the *Abietineae* for instance. But the gradual transition between sporophylls and foliage leaves on which Mr. Seward had laid stress was paralleled among the *Pteridospermeae* in which the sporophylls indeed were scarcely different from the foliage leaves. The male sporophylls of *Araucarieae* were admitted to be unlike those of the *Lycopods*, but they were said to resemble the sporophylls of *Cheiro-*

*strobilus*. You could not quite run *Cheirostrobilus* and the Lycopods together. *Cheirostrobilus* was a representative of an enormously ancient synthetic group, and to derive the Araucariaceæ from that was a very different thing to deriving them from ordinary commonplace Lycopods. Professor Oliver in a recent remarkable course of lectures had referred to the possible existence of a very ancient common group from which all the lines of Pteridophytic descent might have sprung, and had suggested that while the Sphenophyllineæ had retained the fertile ventral lobe of the sporophyll, this character might have spread down the Filicinean line of descent and reappeared in the Gymnosperms. This was a bold hypothesis, but it was a very different thing to deriving Conifers from Lycopods. The gap between the Araucariaceæ and the Lycopods was much wider than any gap we should meet if we took the Filicinean view of Coniferous descent. If he had had unlimited time, he would have liked to have made some concessions to Mr. Seward.

He would have liked to point out that he could have supplied  
 9.0 Mr. Seward with better ammunition than he had used.

There were some striking anatomical peculiarities, such as the double leaf-trace in *Sigillariopsis*, the tracheal elements in the medullary rays and the transfusion-tissue in the leaves of both Lycopods and Conifers which undoubtedly supplied points of resemblance between the two groups. The transfusion-tissue might find its explanation in homology with part of the primary wood of Pteridosperms, and the other instances were probably cases of what Professor Lankester had called homoplastic development, especially as they appeared in the higher rather than in the lower groups of Conifers.

After some remarks from the President, Mr. ROBERT BOYD THOMSON (Toronto), rising at 9.7 at the invitation of the President, said that he did not want to join in the discussion, but he hoped to add some difficulties to it. He had been studying the coat of the megaspore (embryo-sac) in Gymnosperms, and his attention had been specially called to the Araucariaceæ. He thought that on the assumption that the Gymnosperms were monophyletic, the thicker the spore-coat the more primitive the group. He found that the coat was very uniform in structure throughout the different groups, consisting of an outer suberised layer, the exosporium, and an inner, incompletely suberised layer, the endosporium. Cycads had the thickest coat and *Ginkgo* came next. Conifers had a coat very variable in thickness; it might be quite thin or even absent, while in Gnetales the coat was very thin. Of the Conifers the Abietineæ had a uniformly thick coat which thinned out at the apex. In the Cupresseæ the coat was much thinner, which seemed to correspond with the specialisation of the group. The Taxeæ had no coat whatever. In Podocarpeæ, *Podocarpus* had none, while that of *Dacrydium* was quite thick. The Araucariaceæ had quite a different type from the rest of the Conifers. The coat was single, the exosporium having disappeared. The endosperm was "rumi-

9.15 nated" and in correspondence with this folding in and out the megaspore had lost its exosporium, just as in the case of the pollen tube which had also to burrow between the cells of the ovule. The megaspore in fact could not be distinguished from the pollen tube, especially when both were in a multinucleate condition. So that the Araucariaceæ were quite isolated in this character. In the vegetative structure there was a resemblance to Cordaiteæ,

as Dr. Scott had pointed out, and in the reproductive organs other primitive features had been recently found. There was the gradual transition from vegetative leaves to the sporophylls in the Araucarian cone. The sporophylls were green in colour like the foliage leaves. The pith increased in the Araucarian cones, both male and female, again relating them to the Cordaitæ. The number of microsporangia was large and indefinite. Their structure was peculiar in the fact that they had a diffuse annulus and a well-defined stomium. The wall was as much as seven or eight cells in thickness and had resin-ducts giving a hint of synangial origin, the microsporangia being surrounded by tissues similar to those of the sporophyll. The vascular supply to the microsporangia gave indications of homology with that to the megasporangia, taking into account that the former were borne on the lower and the latter on the upper surface of the sporophyll. Instead of falling into the micropyle the pollen of *Araucaria* fell on the sporophyll near the end of the ligule and the tube grew backwards into the micropyle. At certain stages the sporophylls were found to be covered with these tubes. *Agathis* on the other hand had no ligule and the pollen grains fell on the sporophyll nearer the micropyle. The supernumerary nuclei found in the pollen grain of *Araucaria* by Lopriore were not, as he supposed, generative nuclei. Two generative cells could be observed quite distinctly side by side. The other nuclei might have been developed from the tube nucleus in relation to the unusual length of the tube, but more probably represented primitive prothallial tissue. The development of the embryo was peculiar, being intermediate between that of Cycads and *Ginkgo*. The megasporangium, as was well-known, had an inversely oriented vascular supply. In a certain species of *Agathis* there were two sets of lateral bundles with no destination, which were also inversely oriented. Professor Jeffrey had found a cretaceous type which he called *Proto-Dammara* with three ovules on the megasporophyll. The lateral bundles in *Agathis* were probably the remnants of the supply to similar lateral ovules.

MR. CARRUTHERS said that he came as a learner to hear Dr. Scott's account of recent work. He had no doubt of the existence of true ferns in the Carboniferous apart from the Medulloseæ. 9.30 He could not help thinking that the search for common ancestors introduced a difficulty. It would have been better if Dr. Scott had confined himself to determining affinities.

PROFESSOR F. E. WEISS (Manchester) said he was sure most of them were anxious to hear Mr. Seward's reply to Dr. Scott's arguments. Although he had not had the advantage of being present on the last occasion, he had read Mr. Seward's account of his views. He himself had been accused by Dr. Scott of sitting on the fence and had been requested to get down on one side or the other. Now he had been brought up in a way which tended to make him espouse the Filicinean theory of Gymnosperm descent, but they had all been waiting for the publication of Mr. Seward's work on the Araucariæ to see what evidence would be brought forward, because they knew that Mr. Seward had seen reason to believe in the Lycopodincan descent of this group at least. All of them agreed that the work of the last ten years or so had put the Filicinean origin of Cycads beyond question. This probably applied to Cordaitæ also, and Mr. Seward's own work had helped to make

the Cycadean and Cordaitan affinities of *Ginkgo* clear. There remained the Taxaceæ. The seed of *Torreya* shewed clear indications of Cycadean affinity, and he would be inclined to take all the Taxaceæ as allied to *Ginkgo* and descended from a Filicinean stock. As to the Araucariæ and the Abietinæ, there was much to be said for separating them, and also for keeping them together! The Araucariæ were undoubtedly a very ancient group. Dr. Thomson's researches had strengthened his belief in their Cycadean affinities. The inflorescence and seeds pointed in the direction of Filicinean descent and so did the microsporangia and the embryo. He had, however, some undescribed fossil fragments which combined the characters of Coniferous and Lepidodendrean wood. According to Renault *Sigillariopsis* had pitted tracheids; but bordered pits must have descended from scalariform within the Filicinean phylum and there was no reason why they should not have done so on the other line also. They now had a much wider field than formerly from which to derive the Conifers. Nearly every group of carboniferous Cycadofilices turned out to be seed-bearing, and that made their task much more practicable. As to the Abietinæ he must say he was in favour of considering them allied to the Araucariæ, though, perhaps, not so closely as used to be thought. It would indeed be extraordinary if we were to derive all the other groups of Coniferæ from Cycadofilices and the Araucariæ alone from Lepidodendreæ, from which they differed so much in certain respects.

DR. A. B. RENDLE (London, British Museum), speaking from experience of the recent forms, said that the Abietinæ, Cupressinæ and Araucariæ naturally held together, while they formed a  
**9.45** strikingly distinct group from the Taxaceæ. He should not be sorry to have an additional reason for emphasising this distinction. Both Mr. Seward and Dr. Scott had, in his opinion, made out very good cases for their respective views.

MR. W. C. WORSDELL (Kew) said that Mr. Seward was one of those with whom he periodically disagreed, and that radically. To deal first with the question of the relation of the Araucariæ to the other Conifers. He had himself worked a good deal at the Araucariæ, but it had never occurred to him that there was any great difficulty about them. *Araucaria* might be a puzzle to the monkeys, but he declined to be faced with a fresh difficulty in the matter himself. What they had always to consider in these cases was the *tout ensemble* of the characters of the reproductive and vegetative organs, and this undoubtedly shewed a likeness to the Abietinæ. The reason why Sachs, Eichler, Potonié and Seward had considered the Araucariæ as allied to the Lycopods was because they had taken a detail here and a detail there and laboured these, instead of taking a broad view. They had entirely failed to make use of any insight they might or might not have possessed. It was easy enough to find relationships if you merely attended to details; that was the way it was done; but such relationships were quite valueless. Unfortunately, no teratological phenomena, on which he always laid great stress, were known in the Araucariæ, but they were in the Abietinæ and shewed that the single ovule was a modification of an axillary shoot bearing sporangia. Having got that conclusion, we could trace a relation to the Taxaceæ, thence to *Ginkgo*, and thus to the Fern phylum. He would tell them the grain of truth underlying Mr. Seward's view, for there was a grain of truth underlying even that. All

groups of plants shewed the *same* organs because they had inherited them from common ancestors, and that was why it was possible to make plausible false lines of descent. What was mainly wanted was to study *living* plants and to take broad views. He did not wholly deprecate the Micawber-like attitude of certain botanists of palæobotanic tendency in hanging round the mouths of coal-pits and waiting for something to turn up, but they must in the first place study living plants, applying the first principles of morphology to the determination of their relationships. They had plenty of instances of the persistence of ancient characters side by side with derived characters. It was certain that homospority must be older than heterospority, for instance, but plenty of homosporous ferns still existed, and the same thing occurred in the Equisetum and Lycopod groups. The Ophioglossaceæ were very interesting because they combined the characters of the Fern and Lycopod phyla. They were the persistent remnants of the generalised types which were the common ancestors of the Lycopods and Ferns. *Isoetes* occupied a somewhat similar position, but had predominantly Lycopod characters. The ligule of the Araucariæ was no doubt homologous with that of the Lycopods, but that did not mean that the one group was necessarily derived from the other.

MISS E. N. THOMAS (London) said that an extended series of observations on seedlings had led to the conclusion that the arrangement of the vascular system in the cotyledons, hypocotyl and primary root would probably, in future, be regarded as of considerable taxonomic value. As regarded Gymnosperms there seemed to be a Cycadean type derived from the study of seven out of the nine genera. In this type there were usually four bundles at the base of each cotyledon. A tetrarch root was formed, which generally became diarch lower down. This type was also found in *Araucaria*, and outside these groups could only be paralleled in *Ginkgo*. So far as this evidence went, therefore, the vascular structure of the seedling confirmed the affinity of *Araucaria* with Cycads and *Ginkgo*.

PROFESSOR F. W. OLIVER (London), rising at 9.57 to reply, said the discussion had followed the course that might have been expected. Diversity of view, inevitable in discussing questions of origin, had shewn itself and been happily expressed. That Cycads shewed close Filicinean relationship was agreed to on all sides, but on the other hand Mr. Seward's view of the Lycopodinean affinities of the Araucariæ and of other Coniferæ too had met with opposition. He had been glad to hear Dr. Scott call attention to the fact that Mr. Seward had wandered from the Lycopods to *Cheirostrobus* which was a totally different thing. This brought him to the contribution of Mr. Worsdell, and he found himself in substantial agreement with a great deal, and that the most important part, of

**10.0** Mr. Worsdell's speech. No one supposed that the documents on which we relied did not go further back than we could trace them, and the probability of the existence of ancient groups of which we had no trace came out when we considered, for instance, the suggestion of Sphenophyllinean sporophylls contained in the male flowers of *Cordaitea*. There was also a resemblance between the division of some Cordaitean and some Sphenophyllinean leaves. Bearing in mind these facts he need not say how heartily he agreed with the general tenor of Mr. Worsdell's remarks about a common group representing the ancestors of the Sphenophyllineæ, Equisetineæ and Lycopodineæ on the one side and of the Ferns on

the other. But it was one thing to admit freely that a very old character which had been mainly seen in one branch might, so to say, be carried a very long way along the stream of the other, and might eventually appear in an offshoot of that other, and quite another thing to suppose that a member of the one branch was derived from a member of the other. He repudiated entirely the origin of *Araucariæ* or of any known *Gymnosperms*, from *Lycopods*. Altogether, the more he scrutinized that proposal, the less conviction it carried.

MR. A. C. SEWARD (Cambridge) said that at that late hour he rose, in rather a battered condition, to reply to many remarks and some arguments. Professor Weiss had rather exaggerated his (the speaker's) position. All he had ventured to do was to bring forward arguments in support of a theory which was not, of course, his own, but had been well-known for many years. The result of the discussion had been that he still held the views at which he had arrived quite as strongly as he had done seven weeks before. The question at issue had, he thought, been somewhat obscured by some remarks of Dr. Scott. He had previously emphasised the fact that he was dealing not with the *Coniferæ* as a whole but with the *Araucariæ* alone. He did not say anything about the *Taxacæ*, or about *Ginkgo*, being derived from *Lycopods*. He did not consider *Ginkgo* a *Conifer* at all, but would place it, as had recently been done, in a class by itself. Too much stress had, in his opinion, been laid on such a relatively minor point as the form of pitting of the tracheids as shewing relationship between *Araucaria* and *Cordaite*s. Professor Weiss had stated that it was easy to derive the megasporangium of *Araucaria* from that of *Cordaite*s. He could only say that he did not find it so, but thought the derivation from *Lepidodendron* or *Spencerites* much easier. With regard to the *Abietinæ* he ventured to think that if it had not been for the abundant crop of monstrosities produced by that family far less would have been heard of the "axillary shoot" theory of the ovule from Celakovsky and Mr. Worsdell. He thought it probable that *Abietinæ* might be related to *Araucariæ*. With regard to the remarks of Miss Thomas about the seedling structure, it was very difficult to know exactly what weight should be attached to such evidence in phylogenetic questions, but he had no doubt that in the whole discussion too great stress had been laid on vegetative, and too little on reproductive organs. The discussion had well served its purpose, because it had enabled them to get a somewhat clearer idea of the questions at issue.

The PRESIDENT in closing the discussion remarked that the 10.15 original speakers were evidently all "of the same opinion still" at the end of the debate, and non-experts had had their ideas thrown into a good deal of confusion. The only contribution he could make to the question was to suggest that zoologists generally found it a safe guide when considering the phylogeny of groups of animals to attach the greatest importance to those characters which were of the least importance to the animal in its every day life.

[*The Meeting was then adjourned.*]

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PROBLEMS IN AQUATIC BIOLOGY, WITH SPECIAL  
REFERENCE TO THE STUDY OF ALGAL PERIODICITY.

BY F. E. FRITSCH

(University College, London).

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THE study of Botany, like that of Zoology, has gradually passed from a purely descriptive and classifying stage to a morphological or physiological consideration of the diverse organisms and their vital functions. For many years the Morphologist and Physiologist worked apart and in their segregated seclusion failed to recognise how the results which they obtained were really of most importance when considered jointly. The Ecologist has been the happy means of uniting these two branches of the subject into one, the aim of which is to determine the exact relations between the plant and its habitat, to show how the special physiological processes of the plant are tuned into unison with the conditions of the environment and to identify the special structural features of the plant with its particular physiological functions. Ecology is not a new branch of Botany; it is merely the offspring of the fruitful union of Morphology and Physiology. In the last two decades many have turned their attention to this aspect of Botany and a considerable amount of information has been accumulated. Our entire knowledge, however, centres about the terrestrial flora and the aquatic Phanerogams, whilst freshwater Algæ have received little or no attention. The purpose of the present communication is to indicate some of the problems with which we are confronted at the outset of the study of Algal Biology, and some means towards their solution. The field is so large a one and there is such a diversity of problems, that much can be done in a fairly limited amount of time, although the main points will require years of patient observation till an adequate solution is obtained.



As in the case of terrestrial vegetation we can consider freshwater algal growth from several points of view. We may in the first place merely compile a list of the species occurring in any piece of water, or in all the waters of a given area, *i.e.*, determine its flora; such floras are of considerable phyto-geographical and systematic value, but in their present condition go little further. There is a remarkable lack of precision in the large majority of such floras, evident not only in the complete absence of adequate descriptions of the different habitats, but also in the lack of data regarding the relative abundance of the different forms. A true flora must be able to call up a picture of the vegetation of the district dealt with; it must point out to us what are the important and characteristic forms and must correlate them with the habitat. Then only is it of any ecological value; if more precision in these directions had been employed in the past years we should start the ecological study of freshwater algal vegetation better equipped than is the case.

In the second place we may study the aspect of the aquatic flora, *i.e.*, arrange the species composing it, in their relative order of abundance as dominant and subordinate forms. This can only be done satisfactorily by examining the vegetation in question at frequent intervals in the course of a complete year (or better still of a number of years), although hand-in-hand with such complete observations casual examinations of other pieces of water are bound to yield good results. If a sufficiently extensive investigation of this kind is carried out it will be found that different pieces of water (often far apart from one another) contain the same dominant and to a considerable extent the same subordinate forms and we shall be able to classify these different waters according to their algal vegetation. A basis of this kind once established we shall in many cases be able to determine to which type a certain piece of water belongs by a single examination of its algal flora. Periodical observation is, however, always a desirable feature of this line of research and the necessary tardiness of this method of observation is compensated for by the fact that it yields numerous other important results on the biology of aquatic growth. It is a familiar fact that in the case of the Algæ a form may be very abundant one month and almost absent in the next (*cf.* the table on p. 164); even in the case of species which persist throughout the year, it is generally found that they are more abundantly represented at one time than at another. These changes in the relative abundance of



an algal species are intimately bound up with its reproduction, the formation of sexual organs very frequently preceding the disappearance or diminished abundance of the species involved (cf. the table on p. 164, and also the chart). Klebs has brilliantly shown in the case of a few algal species<sup>1</sup> that reproduction depends on the realisation of certain external conditions, but at present no attempt has been made at their exact determination in nature; many of Klebs' results depend on conditions which are never realised in nature, although many of them may be paralleled. A comparative study of the same algal species in various pieces of water shows that its period of chief abundance, although frequently coinciding, is not always simultaneous; and the same applies to its reproduction. In some Algæ no doubt these features (*viz.*, maximum abundance and period of reproduction) are influenced by periodically recurring factors (such as the rise of temperature and increase in intensity of light in spring), so that reproduction and maximum abundance are definite periodical phenomena; in other Algæ, however, the factors determining these features are of a more casual kind (*e.g.*, sudden rapid evaporation and consequent concentration of the water) and consequently they do not evidence so regular a periodicity.<sup>2</sup> The only method of precisely determining the time of reproduction of different algal species and at the same time of obtaining accurate information on the natural phenomena which precede and are the cause of reproductive activity, is that of prolonged periodical observation of the aquatic flora of large numbers of different pieces of water, combined with careful notes on the prevailing external conditions. The data thus obtained can then be confirmed by the experimental method, introduced by Klebs, which will form a valuable auxiliary to observations in nature. The method of periodical observation, however, not only enables one gradually to determine the factors influencing reproduction and relative abundance in different algal species (biological factors), for if we take the external conditions influencing any piece of water collectively we obtain an idea of the factors determining the character of the algal vegetation as a whole (ecological factors). The preceding lines merely indicate

<sup>1</sup> Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen, Jena, 1896.

<sup>2</sup> Thus in the case of the algal flora in the pond at Telsecombe which I am using as an illustration in the present paper *Coelochaete scutata* and *Chara* sp. are forms in which reproduction is a definite periodic phenomenon, whilst in *Oedogonium inversum* this is not the case. *Oscillaria tenuis* affords an example of a form in which maximum abundance is definitely periodic (cf. chart on p. 160).

the more important results to be attained by a study of algal periodicity; there are numerous other minor problems, which will also find solution in this line of research, some of which will be pointed out below. For some years past I have been collecting periodic data of this kind with the kind help of a number of provincial Botanists; the arduous task of working through the large mass of accumulated material has been to a great extent undertaken by Miss F. Rieh, who has also contributed materially by her own collecting. The detailed results so far obtained we hope to publish towards the end of the year.

There is still a third point of view from which we can study aquatic vegetation; it is by far the most difficult, and we cannot expect to obtain many results until our knowledge of the above points is more advanced. I refer to the study of the inter-relations between the different members of the vegetation of a piece of water. Statistics obtained from periodical and casual observation will help us to determine these inter-relations precisely, but the conditions involving their existence will only be settled by experiment.

An important question, which presents itself at the outset of the study of Algal Ecology, is the determination of the unit; what are we to call a formation? A terrestrial plant-formation consists of a collection of more or less numerous species, which are all adapted to the same kind of environment, frequently have a similar habit and form a coherent whole. The entire submerged flora of our waters constitutes a biological group, whose chief peculiarity lies in the method of nutrition and gaseous interchange owing to the special conditions of the environment; submerged aquatics are comparable with epiphytes, parasites, carnivores, etc., all of which are biological groups owing their special character to some common peculiarity. The members of these different biological groups are, however, characteristic of diverse formations, since other features of their structure (apart from the common biological peculiarity) adapt them to different kinds of environments; this is most noticeably the case amongst parasites. We are then confronted in the first place by the question: Are submerged aquatics also to be split up and relegated to different terrestrial formations, or in other words, are the species populating a given piece of water dependent on the nature of the surrounding terrestrial vegetation? It is not impossible that there are relations of this kind, but it does not seem likely that they will be fundamental. Probably it will be found that the submerged flora of woodland pools for instance is

not always the same in the same woodland-formation, so that we cannot characterise the latter by a definite type of submerged vegetation in the pools which it includes. There are not sufficient data as yet fully to settle this point, but for the time being at least we must separate the submerged from the surrounding terrestrial vegetation as a distinct formation. The conditions involving the existence of aquatics as a special biological group are of a far more extreme nature than those pertaining to the other biological groups referred to above, consisting as they do in a total change from a gaseous to a liquid environment; and from this point of view, even if it should be found that an aquatic flora is to some extent dependent on the nature of the surrounding terrestrial vegetation, it will be better, in my opinion, to look upon the former as a distinct formation.

Different pieces of water differ among themselves very materially in the nature of the submerged flora, so that we must distinguish a number of aquatic formations. Until a large number of data have been collected by periodical and occasional collection it is impossible precisely to define these formations. But a number of useful points may be indicated.

In the first place we can roughly classify waters into those containing Cladophoraceæ and those in which members of this order are wanting. This is probably a fundamental distinction and is particularly useful, because where Cladophoraceæ occur, they are generally to be met with in some quantity *all the year round*, so that this point is very readily determined. The presence or absence of these Algæ is probably intimately related to the aeration of the water, Cladophoraceæ only occurring in waters, which are not absolutely stagnant. This is a point which is very evident in the Tropics, where, owing to the higher temperature, there is a proportionally smaller amount of oxygen dissolved in the water, so that Cladophoraceæ (except *Pithophora*<sup>1</sup>) are strikingly rare in these parts of the world and generally occur only in well aerated water (*e.g.*, wells, rivers, etc.) There is some evidence that certain species of Cladophoraceæ are able to exist in almost stagnant tropical waters, but the floristic records are too imperfect and unsatisfactory to admit of certainty on this point. The presence or absence of Cladophoraceæ involves other differences, since they constitute one

<sup>1</sup> *Pithophora* is much better able to meet the exigencies of tropical conditions owing to its thin walls, relatively narrow filaments and perhaps also its akinetes. This subject will be dealt with fully elsewhere.

of the most important substrata for the growth of a number of epiphytes (Protococcales and Diatoms), which are wanting or poorly developed when the Cladophoraceous element is lacking.

Admitting a classification of pieces of water into those with and those without Cladophoraceæ, we may next turn our attention to the importance of other groups of Algæ, viz., *Vaucheria* and the Confervales, the Conjugatæ, *Oedogonium*, the Ulotrichales and the Cyanophyceæ. All of these no doubt play an important part as character-plants, but space does not permit of more than a brief consideration of some of them. The peculiar assimilatory process of *Vaucheria* and the Confervales probably makes these forms more susceptible to variations in the environment than most other green Algæ; it certainly seems as though they will rank second in importance to the Cladophoraceæ as character-forms of aquatic formations. These Algæ are very rare in tropical freshwaters (especially *Vaucheria*), although the exact reasons for their scarcity are not yet apparent. Special note should therefore be made of the occurrence or absence of *Vaucheria* and *Conferva* in a piece of water.

The Conjugatæ will undoubtedly also furnish a valuable feature in the determination of aquatic formations; on the one hand the presence or absence of forms of this group is to be noted, but in many cases it will be necessary to apply a more detailed scrutiny, since certain Conjugate species or genera (e.g., *Spirogyra*, *Zygnema*, filamentous Desmids) are certainly of value as character-plants; the same remarks apply to the Diatoms.

Cyanophyceæ are probably also important character-plants; the large majority of the members of this group have a preference for waters of warm temperature, so that they are not found in deep waters, which are not much heated by the sun, and are more characteristic of shallow lakes and ponds. The blue-green Algæ are excessively characteristic of tropical freshwater formations to which they give a very distinctive stamp.

The object of the present communication being only to indicate the lines of research adopted and one or two of the general results, I will refrain from further discussion of details and will only point out that looking at the algal vegetation of different pieces of water as a whole, one notices that some contain a considerable number of broad filamentous forms, while in others the prevailing type is that of a relatively narrow filament. This distinction is probably frequently a fundamental one due to the

relative degree of aeration of the water; poor aeration necessarily excluding forms with broad filaments, especially if these latter have thick walls (as in *Cladophoraceæ*). Air-content is probably as important in the water as water-content is on land.

In characterising our submerged aquatic formations it will be necessary, however, to take the other submerged plants into consideration as well; and it may be that in some cases the formation will be characterised entirely, or in part, by certain dominant Phanerogamic aquatics. On the latter point I do not care to pronounce an opinion as yet, but there is no doubt that certain Algæ and Phanerogams frequently, if not invariably, go together. Thus *Myriophyllum* appears to occur in waters frequented by *Cladophoraceæ*, whilst waters with *Ranunculus aquatilis* seem to be rich in Conjugates (often together with *Microspora*). Other aquatic Phanerogams probably, like many Algæ, are not so particular and occur in a number of different types of water; such forms will be of no value in characterising aquatic formations.

We have next to consider the other types of vegetation, occurring in the water, *viz.*, the floating and the marginal (semi-aquatic) forms. The advisability of separating the floating from the submerged vegetation of a piece of water as a distinct formation is open to discussion; it is almost impossible to establish a sharp delimitation, and, if we resolve to regard the two as separate formations, we shall in many cases be confronted by the anomaly of an individual belonging to one formation in its young stages, and to another in later ones. The floating vegetation of a piece of water constitutes a biological group within a biological group, and is better regarded as an association or group of associations, comparable in some respects to the undergrowth and epiphytic vegetation of a piece of woodland. On the whole it is dependent on the same collection of factors as influence the submerged vegetation of the pond, and often at least its nature depends largely on the character of the remaining aquatic growth. I should propose as a preliminary to distinguish the following associations among the floating vegetation:—

(a) Free-floating Cormophytes, such as *Lemna*, *Azolla*, *Salvinia*, *Riccia*, etc.

(b) Attached Cormophytes with floating leaves, e.g., *Nymphaea*, *Limnanthemum*, *Elisma*, etc.

(c) The Plankton or microscopic (thallophytic) forms, e.g., forms which are free-floating or actively motile throughout the vegetative stage of their life-history,

The second of these associations is difficult to separate from some of the submerged associations (cf. below). A union of (a) and (c) may be suggested and can doubtless be supported, but the separation is useful owing to the fact that the free-floating forms among the higher plants are more or less confined to the littoral region, while the Plankton, as is well known, extends throughout the piece of water from shore to shore. Amongst the Plankton I only include forms which are *never* attached at any period of their life-history. This is a necessary limitation; otherwise it would be impossible to exclude forms like *Spirogyra*, *Cladophora*, etc., which I regard as belonging to the submerged associations. It is not possible, however (at present at least), to define absolutely the limits between the Plankton and the submerged associations in all cases.

In the case of the marginal (semi-aquatic or marsh) vegetation there is much more to be said for looking upon it as a distinct formation. The conditions of life are very different from those of the true aquatics, since only the lower parts of the plant are submerged, whilst the greater portion is sub-aerial. The presence of the marginal zone of vegetation is dependent on different conditions to those which influence the submerged or floating forms, and in many cases (e.g., where the shores are very steep) it may be wanting altogether. All these features, I think, make it desirable to separate the marginal growth as a distinct formation (reed-marsh formation). In many cases it is not easy to delimit it on the land- or on the water-side, but many of our terrestrial formations have equally indefinite boundaries. Every formation is necessarily best developed in the middle of the area which it occupies, and near its limits it will often grade imperceptibly into another formation. In correspondence with the gradually increasing depth of the water the marginal growth often shows a well-marked zonal development; the zones may be regarded as distinct associations which have already been defined by others (Schröter and Kirehner, Magnin) more capable of dealing with them. Similar zones can also frequently be distinguished in the submerged growth, which succeeds the semi-aquatics as the deepening of the water excludes the latter. These associations are, however, dominated by and probably only to be characterised by Cormophytes. A considerable amount of algal growth occurs amongst these latter, but it is very questionable whether there is any marked restriction of algal forms to one or other of these cormophytic associations and, until adequate evidence in support of this is forthcoming, it is better to regard all the littoral algal growth as an algal association distinct from the cormophytic ones.

Before proceeding to deal with the other features presented by the submerged growth it may be well to tabulate the vegetation of a piece of water as follows:—

“A” FORMATION:—Semi-aquatic or marsh vegetation.

(a) *Cormophytic associations* (e.g., *Phragmitetum*, *Scirpetum*) not always present.

(b) *Algal associations* of the “Spritzzone,” i.e., forms growing in well aerated and frequently disturbed water, often subjected to periodical exposure.

“B” FORMATION:—Aquatic vegetation (type of formation dependent on air-content, etc., cf. p. 154).

(a) *Cormophytic associations*.

α. Free-floating (e.g., *Lemna*, *Azolla*, *Hydrocharis*, etc.)

Nupharetum,  
Potamogetonetum,  
Characetum. { β. Attached with floating leaves<sup>1</sup> (e.g., *Nuphar*,  
*Nymphaea*, *Potamogeton*.  
γ. Submerged and attached<sup>1</sup> (e.g., *Potamogeton*,  
*Myriophyllum*, etc.)

δ. Submerged and not attached (e.g., *Ceratophyllum*, *Utricularia*, etc.)

(b) *Algal associations*.

α. Plankton.

β. Submerged growth of photic region (perhaps to be united to α δ).

γ. Submerged growth of aphotic region.

In every piece of water, apart from noticing these different associations, we find examples of more intimate relationships, which I will briefly touch upon now. I have already pointed out above that *Cladophoraceæ* generally bear a growth of characteristic epiphytes and I have no doubt that more detailed investigation than has as yet been possible will show that many filamentous *Algæ* bear epiphytes, more or less restricted to them. The reasons for these restrictions are probably due to a diversity of conditions, presented by the character and mode of life of the *Algæ* bearing the epiphytes, e.g., structure of the wall (with or without a thick mucilaginous investment, etc.), position in the water (near the surface or deeply submerged, in a shaded or exposed position), assimilatory and respiratory activity and consequent amount of excreted oxygen and carbon dioxide, period of maximum abundance, etc. There are

<sup>1</sup> It is possible that β and γ are not distinct associations, but the evidence for their union as Nupharetum, Potamogetonetum, etc. is not quite satisfactory.

doubtless many, so to say, cosmopolitan epiphytes which will grow on any sort of substratum, but a considerable number of them are probably more particular and are influenced by conditions like those just indicated. Nor are epiphytes the only forms exhibiting these features; the tangle of every filamentous Alga affords shelter to a larger or smaller community of Protococcales, Desmids, Diatoms, etc., and there is evidence that here also we have no casual phenomenon, but that many of these forms are confined to the tangles of one or other species of Alga. In some cases (especially in the attached algal growth on submerged rock-surfaces) we find a number of filamentous Algæ densely intertwined with one another to form compact masses, often including a certain number of unicellular forms. Such dense algal felts undoubtedly show much the same composition in pieces of water far apart from one another; their object seems to be in the first place a protective one against the ravages of aquatic animals, but it is quite possible that more important (nutritive?) inter-relations exist, which we are at present not in a position to determine. The preceding remarks will suffice to show the necessity of noticing the inter-relations amongst the different members of the algal vegetation of a piece of water. I have elsewhere proposed the term *consortium* (=fellowship, participation) for such intimate connections of algal forms; there is a closer relation in these cases than between the different members of an association and so a separate designation seems warranted; a consortium carries us half-way towards symbiosis.

I will now return once more to the periodicity of aquatic vegetation. The great difference between the ecological study of terrestrial and aquatic plants lies in the very marked seasonal variations of the latter. In the case of a terrestrial flora the plants, which constitute a formation, are represented in it throughout the greater part of the year; some of them will be more prominent in some months than in others owing to flowering or numerical preponderance, but all persist throughout the greater part of the period of vegetation and are always to be found amongst the members of the given formation. In an aquatic flora on the other hand matters are very different; in most cases a number of dominant forms succeed one another in the course of a year<sup>1</sup> and after their

<sup>1</sup> Cf. the table on p. 164; also Fritsch, *Algol. Notes*. IV. Remarks on the periodical development of the Algæ in the artificial waters at Kew. *Annals of Bot.*, Vol. XVII., No. LXV., 1903, pp. 274—278; and Algæ, in *The wild Fauna and Flora of the Royal Botanic Gardens, Kew. Bull. Miscell. Inform., Roy. Bot. Gards., Kew. Addit. Ser. V., 1906*, p. 190.



period of prevalence is past they disappear either suddenly or gradually. They may remain in small quantity for some time or during the whole year or vanish completely. Apart from the Cladophoraceæ very few of the filamentous Algæ are found to be present all the year round; in the case of the smaller forms (Proto-coccales, Diatoms, etc.) there are more examples of this kind of thing. Even the few forms, however, which are always present, often show a well-marked period of maximum abundance and during the rest of the year they exist in much diminished amount. During the period of complete absence a form is of course represented by its resting-spores, but they sink to the bottom of the pond, are lost to view, and as far as the aspect of the flora is concerned, they are momentarily gone. Aquatic vegetation thus often shews a varying composition according to the time of the year at which it is examined and hence the necessity of caution in drawing conclusions regarding the vegetation of a piece of water from one or two casual examinations, until periodical observation of a number of cases has established a basis to work upon. In the case of an algal formation the character-form or forms may be altogether absent at some times of the year and it will only be when we know something about the subordinate members of the formation that we shall be able to recognise it at these periods. The different phases of a formation require far more consideration in the case of an aquatic flora than of a terrestrial flora. An excellent method of obtaining a picture of the aspects of a pond during a prolonged period of observation is the plotting out for each species of a curve representing its relative abundance (cf. the chart on p. 160).

In a recent paper on "Pond Vegetation," by Norman Walker,<sup>1</sup> eight associations are enumerated as occurring in the Bramhope ponds in the course of a year. Prior to the publication of a more detailed communication on this subject it is perhaps a little premature to criticise; but, from what I have seen in other cases of periodicity, I should not be inclined to describe the successive kinds of algal growth as associations, but rather as phases of one and the same association. I should add that it seems possible that the way in which the different phases succeed one another and their degree of relative importance may often be of considerable value in discriminating between allied algal formations.

Periodicity in aquatic vegetation may be of two kinds, *viz.*, seasonal and irregular. Seasonal periodicity is the result of

<sup>1</sup> Naturalist, October, 1905. No. 585, p. 311.

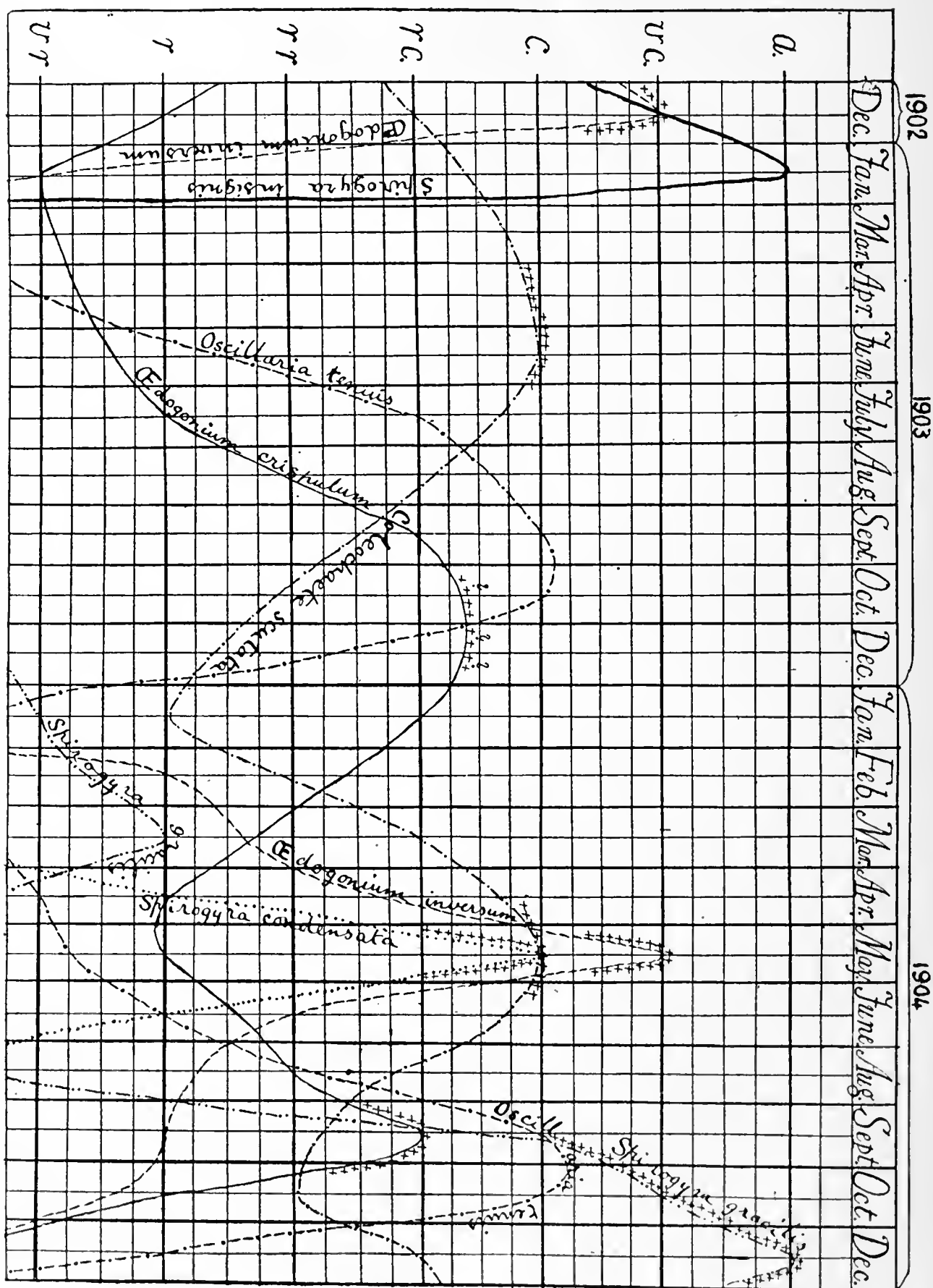


CHART illustrating relative frequency and time of sexual reproduction of seven Algae in a pond at Telscombe.

periodically recurring factors, irregular periodicity of factors, which may occur at any time, although some are more likely to obtain at one season than at another. A brief consideration of these factors may be useful and we will first discuss the seasonal factors. Some of these act directly, others indirectly. Direct seasonal factors are the changes in light-intensity and temperature of water in spring and autumn. The indirect seasonal factors are more numerous; the most important are the seasonal change in dissolved oxygen owing to the seasonal changes in the temperature of the water, the increase in the amount of organic substance dissolved in the water in the course of the summer as a result of the decay of the cormo-phytic aquatics,<sup>1</sup> and of the fall of leaves into the water from the surrounding terrestrial vegetation (hence probably the frequent marked occurrence of *Oscillaria* and certain other Cyanophyceæ towards the end of the summer and in the autumn), the periodic changes in shading from the surrounding terrestrial and the cormo-phytic aquatic vegetation in spring and autumn, the influence of periodic changes in the fauna, and lastly periodic changes in water-level and in concentration of the salts dissolved in the water, wherever there are well-marked rainy and dry periods. All these seasonal factors are no doubt the determinants of the regular periodicity which is manifest in many cases. This regular periodicity is disturbed and often somewhat masked by the irregular factors; the more important of these are varying period of maximum and minimum temperature, abnormal periods of low and high temperature, occasional spells of drought (involving concentration of the water), heavy rainfall (having the opposite effect), periods with strong winds, abnormal spells of dull or bright weather, freezing in winter, and influence of man. In addition to the seasonal and irregular factors we have to distinguish a third set—correlated factors. These represent the influence of the diverse constituents of the vegetation in a piece of water upon one another and are not easy to determine; some of them are seasonal, others are irregular. The most important of the seasonal correlated factors are the shading action of the Plankton on the submerged vegetation (probably a factor more pronounced in the Tropics than elsewhere), and the influence of the disappearance or appearance of one form upon the conditions of existence of another. The latter factor may sometimes also be an irregular one. As an example of a seasonal correlated factor of the former type I may mention the relation,

<sup>1</sup> Cf. Schmidle, Aus der Chlorophyceenflora der Torfstiche zu Virnheim. Flora, Vol. 78, 1894.

which often holds good between *Cladophora* (or *Rhizoclonium*) and the epiphytic Diatoms (*Cocconeis*, *Synedra*, etc.) which it bears. The latter increase to a certain maximum abundance, when they almost completely cover the surface of the green Alga and probably begin to impede seriously the access of the amount of light necessary for assimilation; this leads to a great decrease in the amount of the *Cladophora*, followed by dying off of some of the epiphytes and colonisation of a new substratum by the rest. When the period of least abundance of the epiphytes approaches, the green Alga begins to increase in amount and slowly attains its maximum abundance, but renewed appearance of the epiphytes involves a gradual decrease of the *Cladophora* to a minimum again. In such cases the periodicity of relative abundance exhibited by the *Cladophora* depends intimately on the periodicity of its epiphytes. Irregular correlated factors depend on the co-operation of irregular external factors; in this way the effect of an irregular factor may be multiplied and may involve complicated irregularities, difficult to understand unless the starting factor is known. If periodical observation is to be of avail in biological investigations every care must be taken to secure adequate data regarding all possible factors. In addition to the external factors the inherent tendency of the plant has to be taken into account; but nothing can be said on that point till our knowledge of the influence of external conditions is more advanced.

In determining the conditions for the development of the flora of any piece of water we still require a knowledge of other factors; we may call them the determining factors. Such are for instance the geological formation in which the piece of water occurs, and its altitude, the chemical composition of the water, the maximum depth and relative inclination of the bottom, the relative exposure to sun, shade, wind, etc., the nature of the fauna, the relative air-content, the nature of the banks and bottom, the nature of in- and outflow and possible human influence (e.g., sewage, etc.) A knowledge of these factors is also necessary for a proper interpretation of periodicity, but they are of primary importance for ecological purposes.

In collecting periodical data I have during the last years forwarded to those Botanists who have had the kindness to assist me schedules with questions, one of which has been returned with each sample of Algæ. The questions are as follows:—

- (a) What Phanerogamic aquatics are present, in what amount,

attached or free-floating; sterile, flowering or fruiting, healthy or unhealthy.

(b) Amount of Algæ present; attached or free-floating; healthy or unhealthy in appearance.

(c) Temperature of water and air.

(d) Changes in shading by surrounding plants and of muddiness of water.

(e) Changes of water-level.

(f) Animal life present.

(g) General character of weather in preceding week or fortnight (wind, rain, temperature, sunlight).

If these questions are carefully answered each time, one obtains working data of considerable value. The collection of what I call a representative sample is, however, also requisite to make such observations useful; a representative sample must contain all the different kinds of algal growth in roughly the same proportions as those in which they occur in the piece of water. As a rule the quantity of algal growth abstracted should be very small in amount, so as to avoid introducing a disturbing factor; in pieces of water with a poor vegetation, this disturbance is rather difficult to avoid, however, unless the flora be directly examined on the spot with the help of a travelling microscope. In collecting a sample the entire water must be carefully scanned, while the stems, leaves, etc., of Cormophytes and the surface of rocks must also be subjected to scrutiny; the method of algal collecting is, however, adequately described in all the leading text-books (West, Chodat, etc.) and need not be further dealt with.<sup>1</sup> No great knowledge of Algæ, but care and precision are the requisites for making a good collection. Naturally the smaller the piece of water the easier is the gathering of a representative sample, and I have hitherto almost confined these investigations to small ponds.

In illustration of some of the remarks made in the preceding pages and to show the mode of dealing with a series of periodical observations, I propose to discuss briefly the algal flora of a pond at Telscombe, near Newhaven, from which my friend, Mr. L. A. Boodle, F.L.S., was kind enough to collect a series of samples, unfortunately interrupted during my absence in Ceylon. The first samples were taken from this pond towards the end of December, 1902; at that time there was a rich algal flora, composed in the main of two filamentous species, viz. *Oedogonium*

<sup>1</sup> Cf. also Suggestions for beginning Survey Work on Vegetation. New Phytologist, Vol. IV., No. 4, April, 1905, pp. 101, 102.

1902.

1903.

1904.

	26 XII. t ?	25 I. t ?	8 III. t ?	12 IV. t ?	1 VI. t ?	28 VI. t ?	Aug., Sept., Oct., Dec.	23 I. t 33°	14 II. t 41°	20 III. t 48°	20 IV. t 61°	15 V. t 70°	26 VI. t 71°	10 VIII. t 70°	18 IX. t 58°	30 X. t 48°	26 XII. t 36°
1. <i>Spirogyra insignis</i> var. <i>Brannii</i>	ve.	a.	—	—	—	—		—	—	—	—	—	—	—	—	—	—
2. " <i>gracilis</i> ...	—	—	—	—	—	—		vr.	vr.	f.	—	—	—	—	e!	a!	a!
3. " <i>condensata</i> ...	—	—	—	—	—	—		—	—	—	f.	c.!	f!	—	—	—	—
4. <i>Cosmarium Botrytis</i> ...	f.	f.	f.	rr.	f.	f.		rr.	vr.	f.	f.	f.	vr.	f.	f.	—	f.
5. " <i>graciatum</i> ...	re.	re.	re.	rr.	—	—		re.	f.	re.	rr.	f.	f.	re.	rr.	f.	—
6. <i>Closterium moniliferum</i> ...	f.	—	re.	f.	rr	f.	No	re.	rr.	re.	i.	i.	rr.	rr.	—	vr.	—
7. " <i>acerosum</i> ...	—	—	—	—	—	—		—	—	—	i.	—	—	re.	—	vr.	f.
8. <i>Ulothrix</i> sp. ...	f.	f.	rr.	—	—	—	Samples	—	—	—	—	—	—	—	—	—	f.
9. <i>Oedogonium inversum</i> ?	ve.!	vr.	—	—	—	—	Collected	—	f.	f.	vc.!	ve.!	rr.	f.	f.	f.	—
10. " (cf. <i>crispulum</i> ) ...	f.	vr.	f.	f.	f.	f.	from	re.	f.	f.	f.	f.	rr.	rr.	re.!	f.	—
11. <i>Colcohaete scutata</i> ...	re.	c.	c.	e.	e!	re.	Aug.—Dec., 1903!	f.	f.	e.	vc.	c.!	re.	re.	rr.	rr.	re.
12. <i>Ineffigiata neglecta</i> ...	f.	f.	re.	re.	re.	re.		f.	f.	f c.	i.	e.	c.	re.	rr.	f.	f.
13. <i>Scenedesmus acutus</i> ...	—	—	—	—	—	vr.		—	—	—	—	—	—	re.	rr.	vr.	—
14. <i>Pediastrum Boryanum</i> ...	—	—	—	—	—	—		—	—	—	—	—	—	vr.	vr.	—	—
15. " <i>Ehrenbergii</i> ...	—	—	—	—	—	—		—	—	—	i.	—	—	re.	rr.	—	—
16. <i>Vaucheria</i> sp. ...	—	—	—	—	—	re.		—	—	—	—	—	—	—	—	—	—
17. <i>Oscillaria tenuis</i> ...	—	—	—	vr.	re.	re.		—	vr.	—	vr.	vr.	f.	re.	c.	c.	f.
18. <i>Naevicula lanceolata</i> ...	—	re.	rr.	f.	—	re.		e.	—	—	i.	—	—	—	rr.	f.	vr.
19. <i>Gomphonema olivaceum</i> ...	e.	—	rr.	f.	—	—		—	—	—	—	—	—	—	—	—	—
20. <i>Pinnularia</i> sp. ...	—	f.	—	—	—	—		—	f.	vr.	—	—	—	—	f.	—	—
21. <i>Englena</i> sp. ...	f.	—	—	f.	—	f.		—	—	—	vr.	—	vr.	f.	—	f.	—
22. <i>Chara</i> sp. ...	re.	e.	e!	e!	e.	c.		re.	c.	a.	c.!	c.!	c.!	e.	—	—	—

TABLE showing relative frequency of typical *Algae* in pond at Talscombe, near Netchaven. (Coll. L. A. Boodle).

a, abundant; vr., very common; c., common; re., rather common; rr., rather rare; f., rare; vc., very rare; i., isolated.

A! after the letter indicates sexual reproduction.

Temperature (t) in degrees Fahrenheit.

*inversum*, Wittr., and *Spirogyra insignis* (Hass.), Kütz. var *Braunii*, Rabh. Of these the former species formed flocculent coverings on leaves and stems of *Potamogeton* and *Myriophyllum*, the filaments of the Alga bearing large quantities of *Gomphonema olivaceum* and containing numerous well-developed oogonia. The *Spirogyra* formed floating masses round the edge of the pond, and was not in quite a healthy condition. No smaller forms were included amongst the masses of these two Algæ, which were practically pure. The second sample was collected about a month later (Jan. 25th, 1903), and shewed that considerable changes had taken place. The *Oedogonium* (and its epiphytic *Gomphonema*) had practically disappeared, together with the *Potamogeton* on which it was growing; this may, in part, have been the result of the severe frost which occurred in the weeks previous to the collecting of this sample, but the occurrence of oogonia in the previous month indicated the probable subsequent disappearance of the Alga. The *Spirogyra*, on the other hand, had evidently withstood the frost quite well, and was, if possible, more abundant than before; it now, however (as Mr. Boodle informed me), occurred as a large floating mass, round about *Myriophyllum* in the middle of the pond, and presented the same slightly unhealthy appearance as in the previous month. A week or so previous to collecting the third sample (March 8th, 1903), Mr. Boodle paid a visit to the pond and observed that the *Spirogyra* had decreased very much in amount, and an examination of the third sample showed that it was entirely wanting. The exact causes which led to its disappearance are not quite obvious; it has already been pointed out that it was not in a perfectly healthy condition on the previous occasions and it is possible (even probable) that it underwent conjugation in the (unfortunately prolonged) interim, which elapsed between taking the second and third samples. No trace of either species was observed in the subsequent samples, taken in 1903, although of course either or both may have flourished in the second half of the year, in which no samples were taken. During the whole period another species of *Oedogonium* (*O. crispulum*) was observed in small quantity in the monthly samples, although it never became common and remained perfectly sterile; from analogy with what happened in 1904, it probably developed sexual organs in the latter half of 1903. The first sample collected in 1904 (Jan. 23rd), again revealed a little of this same *Oedogonium* on *Myriophyllum*. There were just traces of a *Spirogyra* (*S. gracilis*) which, however, was a much

more delicate species than the one which flourished in the pond at the same time in 1903.<sup>1</sup> Mr. Boodle had visited the pond earlier in the same month and informed me that there was then a considerable amount of *S. gracilis* in it. In the samples taken on Feb. 14th and March 20th, 1904, matters were much the same, the *Oedogonium crispulum* remaining sterile, whilst *O. inversum*, which occurred so abundantly in the winter of 1903, began to put in an appearance. In the next month (April 20th, 1904) I was much astonished to find that this latter *Oedogonium* had increased very largely in amount and bore numerous oogonia; the *Spirogyra gracilis* became replaced by another species of the same genus with broad short cells (*S. condensata*). On May 15th, whilst *Oedogonium inversum* still occurred as the most prominent form and bore numerous oospores, *Spirogyra condensata* had also become a great feature of the algal vegetation: the latter Alga was in part vegetative, in part however passing over to a condition of fructification exhibiting lateral conjugation. The fact that both the *Oedogonium* and *Spirogyra* were in a sexual condition led one to expect that these species were near the end of their development, and a glance at the next month's sample (June 26th) shows that this was really the case; *Spirogyra condensata* had then quite disappeared from that part of the pond which it occupied on May 15th, although a small patch of it was still present on one side. The next sample, collected on August 10th, showed no trace of the *Spirogyra*, although the *Oedogonium* persisted in small quantity.—During this whole period, as in the previous year, the other species of *Oedogonium* (*O. crispulum*, Witr. & Nordst.) was observed in small amount; in the sample taken on September 18th, 1904, finally it was found to be rather commoner and to be proceeding to form oogonia; six weeks later however (October 30th) it had practically disappeared and was probably in the resting condition. The sample of September 18th showed another interesting feature, viz. the great development of *Spirogyra gracilis* (Hass.) Ktz., which together with the *Oedogonium*, formed the dominant algal form and like it showed indications of the commencement of the sexual process. However it managed to persist, and to become even commoner in the subsequent months and was still the most abundant form in the pond on December 26th; during the whole of this period

<sup>1</sup> The pond was covered by a sheet of ice when this sample was taken, so that its collection was a difficult matter, and it is possible that there was really a larger amount of the filamentous species present than the sample indicated.



zygospore-formation was going on. Judging from analogy, it probably disappeared at the commencement of the next year.<sup>1</sup>

In this pond we must therefore distinguish at least three species of *Spirogyra* and two of *Oedogonium*. The first species of *Spirogyra*, *S. insignis* (Hass.) Ktz., which flourished in December—January, 1902-3, disappeared completely and has not subsequently been observed. It must remain an open question as to whether it has developed zygospores, which are passing through a prolonged resting-period, or whether owing to some cause or other it became completely exterminated in the early part of the year, 1903. The second species,—*S. gracilis* (Hass.) Ktz.—was first observed in the winter of 1904 and had possibly flourished during the last months of 1903 (cf. September to December, 1904); it then disappeared from March to August, 1904, reappearing again in September, from which time onwards it flourished till the last of the samples on which these observations are based was taken. The third species of *Spirogyra* (*S. condensata*) was first observed in the spring of 1904, attained its maximum in May, and disappeared again by July. With reference to the two species of *Oedogonium*, the first (*O. inversum*) occurred abundantly in the winter of 1903, but not at the same period in 1904, whereas it flourished and fruited in the early part of the summer of 1904; after that it again disappeared. The second species, (*O. crispulum*), occurred in slight quantity during the whole period of observation, and was observed to become sexual in September, 1904, (possibly also in September, 1903?), after which it practically disappeared.

The observations recorded in the preceding paragraphs seem to me to bring out two important facts. In the first place the three species of *Spirogyra* attained their maximum at different times of the year, one in mid-winter, one in summer and the third in autumn. This may be due to the inherent tendency of each species or to reproduction in the three cases depending on different combinations of external factors. Comparison with the times and conditions of reproduction of the same species in other pieces of water will help us to settle this point and a number of data of this kind will be submitted in the later publication. The second and more important point is the fact that each time a *Spirogyra* became abundant in the pond a species of *Oedogonium* followed suit (see especially the chart); and still more striking is the point that on two distinct occasions during 1904 (*viz.* May 15th and

<sup>1</sup> It was unfortunately impossible for Mr. Boodle to continue collecting after 1904.

September 18th) were species of these two genera observed to be passing through the sexual stage of their life-cycle at the same time. This seems to indicate, that the same conditions influence the appearance of the species in question and the occurrence of the sexual process in each. This point is so important, that it may be well to define a little more clearly the exact condition of the pond previous to May<sup>1</sup> and September, 1904, *i.e.* previous to the occurrence of the sexual process in these species. Previous to collecting the May sample the weather was very warm for the time of the year and very fine with little or no rain; the water must have become fairly warm on most days (on the day of collecting for instance temperature=70°F.) and the concentration of the dissolved salts probably steadily increased. These may possibly be the more important causes, which led to sexual reproduction; the *Oedogonium*, it will be remembered, already exhibited sexual organs on April 20th, and the April of 1904 was also very mild and fine (temperature of water on April 20th=61°F). It may be pointed out in this connection that the previous year (1903) was very abnormal, being unusually wet and relatively cold (involving the occurrence of a number of irregular factors) and this may possibly be the reason why the phenomena above recorded for 1904 were not also observed in 1903. The weather during the first half of September, 1904, was very cool (temperature of water on September 18th=58°F) and there was a good deal of rainfall; so that in the second case it would seem as though the sudden cooling was one of the stimuli which gave rise to the second sexual process then observed (in *Oedogonium crispulum* and *Spirogyra gracilis*). An important factor in this case was probably also the increase in amount of organic substance dissolved in the water. Alteration in the intensity of the light is also a possible factor in both cases (cf. general discussion above).

We have so far considered only the dominant members of the algal vegetation of this pond, but there are a number of other species, which play a fairly important part in its constitution and we may quite briefly notice them. *Oscillaria tenuis*, Ag. is practically wanting during the early months of the year, but becomes more abundant with the commencement of the warm weather in June (1903 and 1904) when it forms a thin film covering the mud at the bottom of the pond; its maximum development however falls into September and

<sup>1</sup> It should be noted that on this occasion two other species were in the sexual stage (*viz.* *Coleochaete scutata* and *Chara* sp.)

October and was hence only observed in 1904 (cf. my observations on the water-lily pond at Kew<sup>1</sup>). It is thus commonest at the time of the second sexual phase of the pond, if I may be permitted to call it so. *Coleochaete scutata*, growing on the leaves of *Myriophyllum*, is present all the year round like this latter plant; it however attains its maximum development in the first half of the year, becoming sexual in the early part of the summer, *i.e.* during the first sexual phase of the pond.

I hope the preceding pages will suffice to show the multitude of problems in the field of algal biology and ecology and will encourage their study. Many of the points indicated here will be dealt with in greater detail in the subsequent paper and will be supported by actual data obtained from numerous periodic and casual observations. Although much has been said in support of periodic investigation in this paper I do not wish to deny in any way the great value of casual observations, if they are undertaken with sufficient precision. In the elementary condition of our knowledge on these subjects every careful observation is of much value. I have omitted all mention of the analogous problems presented by sub-aerial algal growth; they are however best studied primarily in the Tropics where sub-aerial Algæ play a far more important part than they do with us. A considerable contribution towards this subject is contained in the first part of my paper on the Algæ of Ceylon, which will appear shortly.

<sup>1</sup> Fritsch, Annals of Bot. Vol. XVII. 1903, p. 276.

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#### DESCRIPTION OF CHART ON p. 160.

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Graphic representation of relative frequency and time of sexual reproduction of the more important Algæ in a pond at Telsecombe near Newhaven.  
 — = *Oedogonium crispulum*; —■— = *Spirogyra insignis*; — — — = *Oedogonium inversum*; ..... = *Spirogyra condensata*; — — — — = *Coleochaete scutata*; — — — — — = *Oscillaria tenuis*; — · — · — · — · — = *Spirogyra gracilis*; + + + + + indicates sexual reproduction. *a* = abundant; *vc* = very common; *c* = common; *rc* = rather common; *rr* = rather rare; *r* = rare; *vr* = very rare. (N.B.—No samples were taken during August—December, 1903, so that the curves included in this part of the chart are hypothetical).

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THE OCCURRENCE OF GERMINATING SPORES IN  
*STAUROPTERIS OLDHAMIA*.

By D. H. Scott, F.R.S.

[TEXT-FIGS. 27 AND 28.]

IN 1904 I described in this Journal<sup>1</sup> a specimen showing germinating spores in a fossil Fern-sporangium of Lower Coal-Measure Age. At that time there was no clue to the identification of the sporangium beyond the fact of its Filicinean character. In the following year I was able to describe the sporangia of *Stauropteris oldhamia*,<sup>2</sup> which were found in connection with the fine ultimate



Fig. 27. *Stauropteris oldhamia*. Sporangium containing germinating spores, best shown in the upper part; cf. Fig. 28. The thick inner layer of the sporangial wall is partly preserved. L. A. Boodle phot.  $\times$  about 85.

branches of the rachis. In discussing the affinities of the plant, the question was left open whether it was a member of the true Ferns, such as the Botryopterideæ, or a Pteridosperm, in which case the sporangia would be of the nature of microsporangia.

The object of the present note is to record the discovery of germinating spores in a sporangium belonging to *Stauropteris oldhamia*, an observation which appears decisive in favour of the

<sup>1</sup> New Phytologist, Vol. III., p. 18, 1904.

<sup>2</sup> New Phytologist, Vol. IV., p. 114, 1905.

reference of this plant to Filicineæ, or at least to weigh heavily in that scale.

In examining the sections of *Stauropteris* sporangia, appearances indicating the probability of germination had been noticed for some time past. The first indication was the variation in the size of the spores in different sporangia, a fact which is observable in the illustrations to the *Stauropteris* paper,<sup>1</sup> though its importance was not recognized at the time. Subsequently it was found in several cases that the spores in certain sporangia were in a swollen and burst condition, suggestive of ill-preserved stages of germination. Decisive evidence, however, was only obtained when the sporangium shown in Fig. 27, came under observation. It occurs in a section of a nodule from Shore-Littleborough, Lancashire; the material, which, except for Stigmarian rootlets, is almost pure *Stauropteris oldhamia*, is the same which yielded the sporangia in connection with

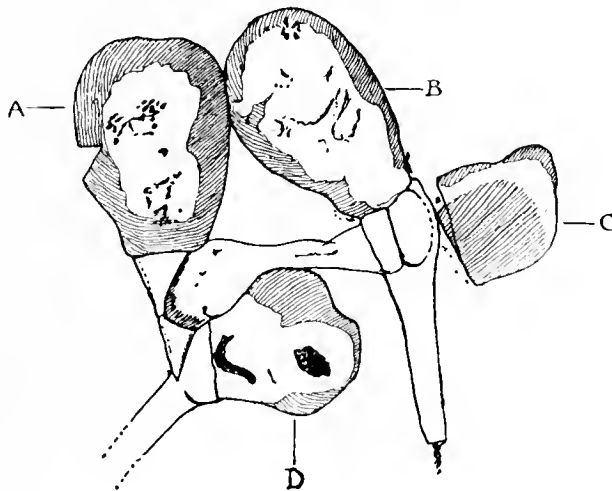


Fig. 28. Four germinating spores from the sporangium shown in Fig. 27. For description see text. From drawing by Mr. L. A. Boodle.  $\times 335$ .

the rachis, described in my previous paper. The characters of the sporangium are precisely the same as those of the specimens in which the attachment is shown. Its length is  $750\mu$ , and width  $580\mu$ . The outer layer of the wall consists of the square or columnar cells usual in *Stauropteris*; the inner layer is only partially preserved; it appears to have been of considerable thickness, though this may be exaggerated by the contraction of the included mass of spores. The smallest spores, apparently ungerminated, measure as little as  $32\mu$  in diameter; those which were already in course of germination are swollen, their transverse diameter approaching  $50\mu$ . A considerable number are in the germinating condition; four of the

<sup>1</sup> Loc. cit., 1905; Fig. 2. Compare the spores in A and B with those in C.

clearest cases, from the upper part of Fig. 27, are shown more highly magnified in Fig. 28. They are overlying each other in various directions, and it is not always easy to trace the parts belonging to each, but I have satisfied myself that the following account represents the facts. The spore A has sent out a narrow outgrowth (incomplete below) which no doubt represents a rhizoid, and is cut off by a transverse wall from the body of the spore. In B the rhizoid extends a good deal further, and appears to be shrivelled at the end, so that it was no doubt longer in nature. In C, which is lying nearly horizontally, the body of the spore has split away from the germ-tube, the upper end of which is cut off as a distinct cell, while the cell-wall at this end of the rhizoid appears to be thickened where it overlies the germ-tube of A. In D the rhizoid is incomplete and is separated by an oblique wall from the spore. On the whole the stages of germination shown in this sporangium are somewhat earlier than some of those previously figured.<sup>1</sup> So far as they go, however, they conform to the Fern-type, and leave little room for doubt that the mode of reproduction of *Stauropteris oldhamia* was essentially that of a true Fern.

The conclusion is important, not only as determining the systematic position of this particular plant, but as throwing light on that of a considerable group. In the mode of insertion of its sporangia, and in its anatomical characters *Stauropteris* approaches the Botryopteridæ more nearly than any other family. Professor Bertrand, who has made a minute study of the vascular structure of the petiole in the whole group, wrote to me, in 1905, that he had no doubt of the relation of *Stauropteris* to the Botryopteridæ, and especially to the genus *Zygopteris*. I am inclined to agree with him in this, though the simpler structure of the sporangial wall in our genus may serve as a distinctive character, for the multiseriate annulus appears to be an important feature in the Botryopteridean sporangium.

The sporangium with germinating spores, described in 1904, has much in common with that of *Stauropteris*, though of considerably larger dimensions, and may not improbably prove to have belonged to another species of the same genus.

In conclusion I desire to express my thanks to my wife, Mrs. D. H. Scott, F.L.S., for her zealous help in the investigation. For the illustrations I am indebted to my colleague, Mr. L. A. Boodle, F.L.S.

<sup>1</sup> Loc. cit., 1904.

# THE NEW PHYTOLOGIST.

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## “BOTANY IN ENGLAND”: A REPLY.

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IN the September number of the *Journal of Botany*, Mr. James Britten deals at considerable length with the portion of my Presidential Address to the Botanical Section at the recent Meeting of the British Association at York, which was printed under the title “Botany in England.”

As Mr. Britten’s criticism seemed based on a misapprehension of the drift of my remarks, and as it was printed in a medium often consulted by Systematic Botanists, I naturally sent a reply which I hoped might be inserted in a forthcoming number of the same Journal. In his capacity of Editor, however, Mr. Britten did not see his way to insert my reply in the form in which I had written it. As I was unable, in my turn, to fall in with the restrictions imposed by Mr. Britten, hospitality for a rejoinder had to be sought elsewhere. It is under these circumstances that the present note appears in the pages of the NEW PHYTOLOGIST.

Whilst welcoming any criticisms that Mr. Britten may think fit to make, I may, perhaps, be permitted to express the hope that the tone which animates his recent utterance may find no permanent place in botanical controversy. When one’s shortcomings are so rudely exposed, there is the temptation to emulate one’s critic and take reprisals.

In my York Address I endeavoured to shew that in the general advance of Botany in this country during the last twenty-five years our great centres of Systematic Botany had become encased, as it were, in a sort of water-tight compartment, and this from causes inherent in their organisation. I do not think it can be seriously questioned that the Herbaria pursue their work apart. One has only to turn to the utterances of men so well qualified to speak for Systematic Botany as Sir George King and Sir William Thiselton-Dyer. The former speaks of its neglect and decadence<sup>1</sup>; the latter

<sup>1</sup> Presidential Address to Section K. Brit. Assoc., Dover, 1899, p. 16.

refers to its decline as a "serious peril<sup>1</sup>." It is not even an open secret, it is common knowledge. Mr. Britten, when his remarks are stripped of the irrelevancies and innuendoes which adorn them, tells us in effect that my apprehensions are groundless and that Systematic Botany jogs on happily without the Schools. Now this is dangerous optimism, or it would be if taken seriously.

The position seems to be this: rightly or wrongly and in spite of warnings we are permitting the Herbaria to become stranded: the Universities, Schools and other institutions which diffuse and stimulate an interest in Botany are not laid under contribution as they might be. Systematic Botany hardly gets its fair proportion of the best that is available. To my mind this is a great misfortune, a source of weakness; nor do I believe I am indiscreet in ventilating the subject. My critic would say, perhaps, "Teach Systematic Botany by all means and then send your people on to us." But that is not the way to get recruits worth having. A mere pious opinion in favour of a given branch of knowledge will effect nothing, even if you put your precepts into practice. If one takes stock of the various places which are centres of activity in turning out students equipped and keen to pursue Science, one finds, with hardly an exception, that those who guide these institutions place original investigations in the fore-front. Heads of departments are selected largely on the strength of their qualifications for research, and so far as circumstances permit support is afforded for its prosecution. Hence, if the great school of Systematic Botany is to be revived in this country, the Systematists themselves, *i.e.*, those with the equipment of the great Herbaria behind them, must take the leading share in the campaign. This was my principal contention at York, and I do not think matters will be remedied until the Herbaria become attached or related in some way to the educational system. Unless our work is to be sterile we must take our share in training those who are to come after us. Robert Brown and Sir Joseph Hooker are exceptions to every rule: if only we could control genius in respect of the time and place of its appearance, all would be well; but experience shews that we have to depend on the normal, and that these two men were not normal is shewn by the fact that none like them have been produced for the past half century.

I should like to see members of Herbarium Staffs *ipso facto* members of the neighbouring University, or, at any rate, a selection from among them. It may be urged that if the Systematist is to

<sup>1</sup> *Ibid.*, Ipswich, 1895, p. 8.



discharge professorial functions it must be at the sacrifice of some of the duties which he at present performs. This is very true. But it was one of my points that much of the routine work which falls to his lot is within the capacity of subordinates. You want two classes in a Herbarium: the scientific workers who would really advance the subject, and subordinates who would carry on a great deal of the routine work. The former would be free not merely to write monographs, &c., along the accustomed lines, but also to open up new lines of attack on old problems. If ever there was a time when the future of Systematic Botany was full of promise, it should be the present. The perfecting of cytological and anatomical technique and the improvement in breeding methods place new implements at its disposal for broadening and deepening its work. Botanists should pull together with a view to so modifying the system that we in this country may take our proper place in the general advance. If we look abroad to centres of activity in systematic work, I think we shall find the relation between the University, the Herbarium, and the Garden, to be an important factor in the case.

When Mr. Britten says I would have Botany the sole possession of the Schools, he falls into error. He depicts me as one who would lock the door and have a bonfire. His readers may rest assured that the unique and precious collections of our Herbaria will suffer no hurt should "men of my stamp" ever get a finger in the pie; nor would the interests of the various classes who consult them be prejudiced. Possibly Mr. Britten has allowed himself to be misled by a too literal interpretation of figures somewhat incautiously employed. My meaning was this: We must not be afraid to go ahead and if necessary modify the line of attack on systematic problems, even if by so doing our present collections should cease to hold the same relative scientific value that they now are supposed to possess. They will always retain their interest; whilst their historic value will ensure their being cherished.

To read his words one might suppose violent annexation of the Herbaria and their eustodians had been advocated. But if Mr. Britten will turn to my Address he will find nothing more revolutionary than a proposal for a working arrangement.

These things, alas, are not burning questions—like District Railway Fares and *The Times* Book Club. Some day let us hope a Minister will arise; one who both sees and cares. The re-adjustment will be effected without a revolution and the only wonder will be that we remained so long on the old lines,

Regarding the question of fusion of the Herbaria of Kew and the Natural History Museum, surely this ancient proposal (which Mr. Britten tells us dates from 1848) may be discussed without emotion. In any case it is of relatively secondary importance and the case for it rests largely on the need of utilizing effectively our resources. My motive in raising it in my Address was the knowledge that unless you pack something concrete into the loading of your gun, the smoke clears off and there is no effect.

On its merits and for reasons already advanced I am disposed to view the proposed fusion with favour, though age and wisdom, according to my critics, are ranged on the other side. As a site, Kew seems preferable for the united Herbaria in view of the contiguity of the Gardens, which offer such unlimited facilities for the attack of systematic problems from the cultural side. The disadvantage of distance is less serious than Mr. Britten supposes, for the students who, it is contemplated, would avail themselves of the improved facilities would be mainly of the post-graduate type, devoting the whole of their time to Systematic Botany. The question of "openings for trained students," by which Mr. Britten means remunerated posts, was never raised by me in this connection. It is remarkable what a number of persons, thoroughly trained, remain in the Universities carrying out original investigations from love of the thing, often making considerable sacrifices so to do. This is a hopeful sign for the future of Science, and it affects Botany in common with the other Sciences. Perhaps Mr. Britten will consider whether it is worth while for the Herbaria to lay this source under contribution. All the same, I fully appreciate Mr. Britten's point when he thanks Heaven that the Museum is managed by Trustees. In so far as the Trustees may be regarded as a sort of half-way-house between a Government Office and a University, that is something to be thankful for. Once you make connection between the systematic institutions and the University, the new growth will begin. In time the University will be worthy to enter more fully into the possession of its heritage. Of course an immense part of the work of Kew must remain outside direct University influence. All the same my dream of the future is a modified Kew discharging its economic and imperial functions, and at the same time supporting a great University department. It may not be realized in our time; its development at best must be slow; what we want is a beginning, towards which indeed the way is mostly paved.

F. W. OLIVER.

THE MEETING OF THE BRITISH ASSOCIATION  
AT YORK.

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THE proceedings of Section K at York were pleasant and profitable, though unexciting. The Address delivered by the President, Professor F. W. Oliver, was divided into two parts. The first dealt with the Evolution of the Seed, and was a skilfully balanced and masterly summary of this topic, in the development of which the President's own work has formed one of the chief turning points. In the second the somewhat unusual course was followed of attacking a problem of what may be called botanical "high policy." The particular topic dealt with was the proper function of national herbaria and museums and their relation to active botanical research. Professor Oliver's out-spoken criticism of existing conditions has, not unnaturally, given rise to some dissent, of which evidence may be found in the present number of this journal.

A feature of the meeting was the devotion of no less than three mornings to the discussion of single topics, and the rather careful organisation of these discussions beforehand. The method adopted was to invite some one or more persons to open the discussion of a given subject, by means either of a general address on the present position of the subject or by the communication of papers containing new facts likely to lead to debate. Botanists likely to be in a position to contribute usefully to such a debate were informed some time beforehand of the intention to hold it and were invited to contribute, abstracts of the opening papers being distributed to them as soon as possible, so that they were acquainted with the facts to be disclosed and the lines to be taken before the meeting. Though it is neither possible nor desirable to limit the sectional meetings entirely to proceedings of this type, it is believed that the method described is on the whole productive of the most interesting and profitable results.

Of course the success of any given discussion depends in the first place on the selection of suitable topics of proper scope. There is the danger of selecting too wide a subject, with the result that the different speakers are apt to deal with quite distinct aspects, and unless the opener has the somewhat rare power of drawing all the threads together in his reply, the impression left on the hearers is liable to be rather inconclusive, not to say chaotic. On the

other hand if the subject chosen be too narrow, the treatment is apt to become excessively technical, and the whole discussion is of limited interest, and may even languish in the absence of sufficiently instructed specialists.

The first discussion, which took place on Friday morning, August 3rd, was really divided into two parts. Dr. Scott began, with a comprehensive title—"Some Aspects of the Present Position of Palæozoic Botany," but considerations of time compelled him to limit himself to "the difficult question of the position of the ferns in the Palæozoic flora," "the difficulty arising from the accumulation of evidence showing that most of the so-called Palæozoic ferns were in reality seed-plants." Dr. Scott showed, in his luminous address,—that "a large body of true ferns of a simple type—the *Primofilices* of Mr. Arber—existed in Carboniferous times," while it is probable that true Marattiaceous ferns also existed side by side with these.

#### DISCUSSION ON THE ORIGIN OF "COAL-BALLS."

The second part of the discussion dealt with the formation of the well-known calcareous nodules found in the coal seams of the Lower Coal-Measures.

Professor Weiss, in a preliminary paper, gave a short general account of the nature and occurrence of the coal-balls, from which it appeared that they are calcareous concretions containing petrified plant remains, occurring at very few, perhaps at only a single horizon, and that while shells are not found in the nodules of the seam itself, they are common in other nodules found in the roof. This fact led Binney to suggest that the nodules were formed by solution of the calcareous salts of the shells and their re-segregation round certain centres in the submerged peaty mass of vegetable matter. A similar mode of formation has been suggested for the calcareous nodules (*Dolomitknollen*) which occur in certain seams of the Westphalian Coalfield, where marine shells are found in the shaly roof of the seam. Lomax on the other hand holds that the nodules were not formed *in situ*, but were water-borne to their present position.

Miss Stopes followed and brought forward all the evidence, obtained from her recent work on the subject, in favour of the origin of the coal-balls *in situ*. In the first place there is no crushing of the plant-tissues within the balls, while the coal around is crushed and bends over the balls. Then the same plant can

sometimes be traced in adjacent balls separated by a streak of coal. Again the balls are often very irregular, with sharp edges and fine fragments projecting, so that rolling after even partial fossilisation, as demanded by the "transport theory" seems impossible. The very local occurrence of the pockets of balls is not in accordance with the assumption that they lie in the track of streams. Only one perfect ball has been found in the floor of a seam; this contained *Stigmaria* only, which is in accord with the "growth in place" theory. Analysis also shews that this ball contains more clay than usual, which is what would be expected if it were formed in the floor of the seam. As to the association of the coal-balls with marine conditions, in every case in which the balls occur, marine shells (typically *goniatites*) were found in the roof of the seam. Where the "Gannister" and "Upper Foot" join to form one seam the nodules are found right through the seam, whereas when the two are separate they are only found in the upper one (with the "marine" roof). Experiments with living plants, which were submerged in sea-water with peat and decaying shell-fish, show that the plant-tissue remains perfectly fresh after nine months, while the animals had quite decomposed. The coal-balls are concretions of  $\text{Ca CO}_3$  and  $\text{Mg CO}_3$ , which probably result from the reduction of the sulphates of the sea-water by the decaying plant.

Mr. Bolton of Bristol argued that as there are many marine horizons in the Coal-measures, the coal-balls should on the theory of Binney be more widely distributed than they actually are. He thought that they might owe their origin to the fragmentation of a basement bed of peat. The country was in a constant state of unrest during the Coal-measure period.

Mr. James Lomax brought forward certain facts which seemed to him to support the river-transport theory of the origin of the nodules; for instance that quite different plants are often found in adjacent nodules. He also stated that certain seams bearing coal-balls have no *goniatite* roof-nodules.

Mr. Watson attacked the views of Mr. Lomax, denying that *goniatite* nodules are absent from the roofs of coal-ball seams.

Other speakers having contributed to the discussion, criticising the details of the chemical processes hypothesized by Miss Stopes, Mr. Teall, the Director of the Geological Survey, supported the *in situ* theory and remarked that an enormous amount of sea-water would be required in the process of formation. This might be supplied by diffusion.

Miss Stopes replied to her critics, pointing out that it is not necessary to suppose the presence of goniatites in the roof *always* led to the formation of coal-balls, while the fragments formed by the breaking of a basement-bed of peat might form the starting-points for the concretions.

Professor Potonié read a paper on the "Origin of Coal" in which he showed the close parallelism between the different kinds of coal and the different conditions of modern peat-formation.

#### DISCUSSION ON "THE NATURE OF FERTILIZATION."

The second discussion, on "The Nature of Fertilization," was held jointly with Section D, in the large Lecture-Theatre, at Bootham School. Though many able speakers took part, the discussion suffered, to some extent, from the danger already alluded to, the difficulty of focussing the interest in the case of a very wide topic with numerous aspects and embracing varied details. Few of the speakers really discussed the *nature* of fertilization, they mostly spoke of various details which they had been working at, or which happened specially to interest them. Discussion or debate, properly so-called—the clash of minds—can hardly be said to exist when this course is followed.

Mr. V. H. Blackman opened with an admirably thought out paper, in which he showed that two advantages may be attributed to "gametic union"—"rejuvenescence and the union of two lines of descent." It is probable that both are important, but neither can be considered as universally applicable, in the first place because there are several groups which show no gametic union, and in the second because of the very close relationship of the fusing nuclei in a large number of organisms—particularly in many plants. The observations of Maupas and of Calkins, seem to establish the reality of rejuvenescence. In regard to the union of the character of parents, the theory of the autonomy of the chromosomes has recently gained ground, and Montgomery's view that in synopsis the maternal and paternal chromosomes are united in pairs is now generally accepted, particularly since it is in general accord with the results of Mendelian inheritance. Interaction between the conjugating chromosomes may take place, and the nature and extent of this is a problem to be determined by the results of observations on heredity.

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Professor Calkins followed with an account of the continuation of his former work on the life-history of *Paramoecium* in which he showed that cultures of that organism periodically pass through a crisis in which their power of division is lost, but that in the absence of conjugation with members of another brood, they can be restored to vigour by treatment with various solutions such as extract of meat, brain extract, phosphates, etc. At length, however, there comes a time when no treatment is able to revive the flagging energies of the organisms and they die. Professor Calkins concluded that generally the stimulus of fertilization is necessary to revive the protoplasm worn out by numerous divisions.

Mr. Doncaster gave an account of the behaviour of the polar bodies in parthenogenetic eggs, but the behaviour of these structures is so different in different forms, and the accounts are often so contradictory that very little evidence can be obtained from them as to the nature of fertilization.

Professor Poulton pointed out that he had used the term *syngamy* (invented by Professor Hartog and used by Mr. Blackman in his Paper) in another sense, to refer to individuals which would breed together. He also suggested that the artificial conditions under which *Paramoecium* was living might invalidate the conclusion of Professor Calkins that conjugation was absolutely necessary sooner or later in the life-cycle of these organisms.

Professor Hartog claimed that he had priority in the use of the term *syngamy*, and suggested an alternative word to be used in Professor Poulton's sense. He compared the phenomena known in the orange, *Funkia*, etc., where cells of the nucellar tissue grow into the cavity of the embryo-sac, and under the stimulus of the exceptional nutrition, grow into embryos exactly like normal ones, with Professor Calkins' results.

Dr. Rosenberg described a very interesting case of parthenogenesis among plants in which the two nuclei formed by the first division of the embryo-sac-mother-cell later fused together and so started a generation with the double number of chromosomes. This case is almost exactly parallel with that of the parthenogenetic eggs of *Artemia* among animals.

Professor Johannsen spoke of the relation of "pure race" breeding to Mendelian heredity, and questioned the validity of the evidence for graft hybrids.

Professor Hickson stated that he had failed to find in recent work any further evidence for the belief—now accepted as a dogma

by most cytologists—that the nucleus rather than the cytoplasm is the carrier of the hereditary properties. He referred to the fact that the work of Boveri on the fertilization of enucleate fragments of Echinoderm eggs had been contradicted by later workers, who had found that the larval stages resulting from such fertilizations might exhibit maternal characters.

Mr. Wager suggested that the sexual unions which are absent in such forms as the Cyanophyceæ might be replaced physiologically by the temporary saprophytic mode of life which is exhibited by some of these organisms.

Mr. Blackman, owing to the lateness of the hour, replied very shortly. He pointed out that it was perfectly clear that many organisms exhibited no syngamic process in their life-history, so that very direct evidence was required to prove that it was necessary to other organisms or that it had to be physiologically replaced by some other process. As to the evidence that the nucleus was the carrier of the hereditary properties he admitted that it was very largely indirect, but nevertheless it appeared overwhelming; for additional evidence obtained in recent times he would refer Professor Hickson particularly to the work of Boveri on doubly-fertilized eggs which he had described in his opening paper. He referred Professor Johannsen to the recent well authenticated evidence for the existence of a graft-hybrid between *Mespilus* and *Cratægus*.

#### DISCUSSION ON THE VASCULAR STRUCTURE OF SEEDLINGS.

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The third discussion took place on Tuesday morning and was on the phylogenetic value of the vascular structure of seedlings.

Mr. T. G. Hill read a paper, by himself and Miss de Fraine, "On the Seedling Structure of Gymnosperms." The observations of the authors' were confined to the Coniferæ. The details of the behaviour of the cotyledon-traces in their passage to the vascular cylinder of the primary root cannot be made clear in an account like the present, but it may be stated that the plan of structure revealed shews certain common features, and that the anatomical evidence leads to the conclusion that the cotyledons of the "poly-cotyledonous" conifers are, in some cases at least, derived by splitting from a primitive "dicotyledonous" type. In another paper "On the Seedling Structure of certain Centrospermæ" of whose contents, owing to lack of time, only the briefest indication was given,



the vascular structure of the seedlings of several species belonging to the Amarantaceæ, Aizoaceæ, Caryophyllaceæ, Portulacaceæ and Chenopodiaceæ were recorded and the same type of structure found in all, with the exception of *Allionia*, in which somewhat more complicated phenomena are met with.

Mr. A. G. Tansley communicated some of the results obtained by Miss E. N. Thomas and himself in the course of an extended investigation into the vascular structure of dicotyledonous and gymnospermous hypocotyls. It was pointed out that whether or no the cotyledons are the equivalents of the first leaves of Pteridophytes and the hypocotyl of the first-formed stem, in any case these are well-marked organs in the seed-plants and the legitimate subject of comparative investigation. The different types of "transition" between the collateral structure of the cotyledonary vascular tissue and the radial structure of the primary root-cylinder are found, with a very few exceptions, to be modifications of one great plan, while the exceptions that are known may very possibly be traced back to the same place though recorded cases are at present too isolated for comparative treatment. The most widely spread type is found to be characteristic of various families of dicotyledons and also among Conifers. Among Cycads and Araucariaceæ a more complex type prevails, with a larger number of cotyledonary traces and the evidence leads to the conclusion that the simpler type is derived by reduction through various transitions from the more complex. There is a particularly clear series of this kind demonstrable among the Gymnosperms. The evidence from the more primitive dicotyledons is not at present so unmistakable. Some possible factors that might have brought about the suggested changes were indicated, and stress was laid on the tentative nature of some of the conclusions.

Dr. Scott remarked that among the Filicinean, Pteridospermic and Gymnospermic series there was much general evidence of the primitiveness of megaphylly. Among the Equisetales, Archaealamites and the Devonian Pseudobornias indicated the same conclusion. Only in the Lycopods did we find, apparently, primitive microphylly. Reduction seemed to be an extremely common phenomenon in the evolution of the vascular plants. There was a presumption in favour of the cotyledons of Spermatophyta being leaves because of the transition, shown by the absence of a resting stage in early Cycad ontogeny, between the Pteridophytic and the Spermatophytic types. Unless the cotyledons were leaves this embryo-

logical investigation would lose much of its interest, because it could not be connected with the Pteridophytes.

Professor Jeffrey said that this particular subject was rather out of his region. But the descent of the authors into "the root of the matter" was well advised. He was sure that an investigation of the cotyledons and hypocotyl was important, and this he said with the more confidence because of his own recent work on cretaceous fossils.

Miss Sargant said that she found herself in the somewhat unusual position of agreeing with nearly everything that had been said, except perhaps one thing. She had always been accustomed to consider the herbaceous type as more primitive because it was more plastic.

Mr. T. G. Hill had always considered that the single bundle of each cotyledon dividing into two in order to make the transition was primitive, and for the present he held to that view. One naturally expected to find this if one accepted the homology with Pteridophytes.

Miss Thomas combated Mr. Hill's views and supplemented Mr. Tansley's exposition in several respects, laying particular stress on the elasticity of the loose Cycad type which would permit of evolution in more than one direction, compared with the rigidity of the "tight" dicotyledonous type. Whatever the factors might be that had led to the evolution of the latter it was quite in accordance with morphological experience that some advanced plants should have escaped their influence. She congratulated Mr. Hill on his elegant demonstration of the relations of the "polycotyledonous" to the "dicotyledonous" type in Conifers, with which from her own experience she entirely concurred.

Mr. Tansley, in replying, also congratulated Mr. Hill on his Conifer work and confessed that he had at one time held the same view of the primitiveness of the unifascicular cotyledon trace and diarch root, but had been forced by the pressure of evidence to abandon it, so far at least as the Spermatophytes proper were concerned. If you could derive the Gymnosperms straight from modern Ferns there would be much to be said for such a view. But recent work had demonstrated the great series of Pteridosperms as intermediate, and they were much more likely to agree with the Cycads. How the complex Cycad type originated was, at present, entirely mysterious.

Mr. A. W. Hill, whose paper on "The Seedlings of certain

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Pseudo-Monocotyledons " was read immediately after that by Mr. Tansley and Miss Thomas, sought to show by a consideration of bulbous and rhizomatous species of *Peperomia* and *Cyclamen*, that clues may be obtained to the mode of evolution of the true Monocotyledons, the two cotyledons assuming different functions. Thus, in his view the single cotyledon of the Monocotyledon represents only one of the two cotyledons of the typical Dicotyledon, the other being represented by the first foliage leaf. Miss Sargant found herself unable to accept this view of the matter.

### ECOLOGICAL PAPERS.

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On Thursday morning, after the President's Address, and in the afternoon, several papers were taken, dealing with vegetation in different parts of the world.

Mr. Seward communicated a paper by Professor H. H. W. Pearson of Cape Town, on "Some South African Cycads: their Habitats, Habits and Associates," in which the Cycad region is described and contributions are made to the natural history of *Encephalartos cycadifolius*, *E. Altensteinii* and *Stangeria*. In a letter received by Mr. Seward from Professor Pearson after the paper had been communicated, some observations are recorded which make it probable that *Encephalartos* is pollinated by insects.

Mr. Hugh Richardson read a paper on "The Vegetation of Teneriffe," in which he brought out the zoning of vegetation round the peak of that island and gave some interesting data on the colonisation of lava streams.

Dr. T. W. Woodhead furnished a very complete account of the history of vegetation-study in Switzerland, a country in which this branch of botanical work is in many respects very advanced. Dr. Woodhead's paper was illustrated by an excellent set of Swiss publications on the subject.

Mr. C. E. Moss contributed a paper on the "Succession of Plant-Formations in Britain," in which he dealt with succession on the coast (sand dunes and mud flats) and in lowland peat; also with the woodland, scrub and heath formations on limestone. He pointed out that the open associations at the beginning of a succession are often dominated by one plant, the intermediate associations are composed by many species, while the final closed associations again have typically a single dominant.

## PALÆOBOTANICAL PAPERS.

On Saturday morning a number of miscellaneous papers were taken, among which were two important palæobotanical communications.

Professor Jeffrey dealt with "The Structure and Wound-reactions of the mezozoic genus *Brachyphyllum*," a genus of hitherto doubtful affinity, which was now shown to be an undoubted member of the *Araucarineæ*, mainly from the anatomical evidence of recently discovered material from the Raritan deposits of Staten Island, New York State, with structure preserved by partial charring. One of the most interesting points in the paper was the use made by the author of the "traumatic" resin canals found in *Brachyphyllum*. It appears that this plant produced definite resin-canals in its wound-callus, as the modern *Abietinæ* do, and unlike the ancient or modern *Araucarineæ*. Largely, though not wholly, on this account Professor Jeffrey concludes that this old genus connects the *Araucarineæ* with the *Abietinæ*, removing the former from their somewhat isolated position, and shewing them as undoubtedly coniferous. Mr. Seward, in the discussion which followed, while quite recognising the validity of Professor Jeffrey's demonstration that *Brachyphyllum* is a member of the *Araucarineæ*, found himself unable to accept the evidence of *Abietinæ* affinity, and particularly that based on the occurrence of the traumatic resin-canals. Professor Jeffrey in his reply, remarked that he had only one thing to say in answer to Mr. Seward's criticism—"he jests at scars that never knew a wound."

Professor Weiss described an interesting new *Stigmaria* possessing a considerable amount of centripetal primary wood, so that at first sight it has the appearance of a stem of *Lepidodendron*, though its characteristic periderm with the remains of rootlet cushions attached show that it is undoubtedly of *stigmarian* nature,

## MISCELLANEOUS PAPERS.

Among other papers of special interest may be mentioned Dr. A. F. Blakeslee's two communications dealing with his important researches on "physiological sex" in the *Mucorinæ* and other plants. In the *Mucorinæ* he has recently found that *Phycomyces nitens* may by special methods be made to produce homothallic mycelia in addition to the ordinary heterothallic ones. The sexual character of these homothallic mycelia is however unstable, and no fixation takes place. Dr. Blakeslee's paper was illustrated by a series of beautiful preparations, showing the homothallic and

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heterothallic character respectively of various mycelia. It will be remembered that the terms in question were introduced to characterise the striking sexual behaviour of these fungi, some of which not only refuse to conjugate with hyphæ from the same mycelium but will only conjugate with those from *certain* other mycelia. These types are known as *heterothallic*.

The author also contributed a general paper (which will be found in the September number of the *Botanical Gazette*), on "Differentiation of sex in thallus, gametophyte and sporophyte." In the last case the words *heterophytic* and *homophytic* are used. Thus *Aspidium* is homophytic, homosporangic and homothallic, *Selaginella* homophytic heterosporangic and heterothallic, *Populus* heterophytic, heterosporangic and heterothallic. Investigations are now proceeding on sexual differentiation in the sporogonium of Bryophytes. It is found that if all the spores from a *Marchantia* sporogonium are sown together they produce a mixed crop of male and female plants and the effect of conditions cannot alter this result. It is therefore to be supposed that segregation of sex must take place during the development of the spores. Dr. Lang, Mr. V. H. Blackman and Mr. Gregory took part in the discussion on these papers.

Of purely physiological papers, Professor Bottomley contributed a very interesting account of his successful attempt to inoculate papilionaceous plants with the root-nodule organisms belonging to non-papilionaceous Leguminosæ and to plants of quite different families, those of *Acacia* (Mimosæ) and of *Elæagnus* and *Alnus* being chosen. In another paper, Professor Bottomley showed that the long known effort of sprinkling urine on the floors of greenhouses in order to cause a more luxuriant growth of orchids is due to the presence of both nitrite and nitrate bacteria in the cells of the velamen, which are thus able to utilise the ammonia arising by decomposition of the urine and absorbed along with the water vapour normally condensed by the velamen.

Miss C. B. Sanders, of Oxford, described some experiments carried out in Professor Gotch's laboratory on the local production of heat connected with the disappearance of starch in the spadices of various Araceæ. Her method differed from the older investigations of Kraus and Garreau on the same subject by the use of Dr. Haldane's method of simultaneous estimation of oxygen and CO<sub>2</sub>. Remarks on the subject of this paper were made by Dr. F. F. Blackman.

Dr. Ellis, of Glasgow, described experiments to show that

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ciliation cannot be used as a taxonomic character among bacteria—as has recently been done by Migula—because under appropriate conditions, all the members of such groups as the Coccacæ, Bacteriacæ and Spirillacæ in which this character has been used, can be made to acquire cilia.

Mr. W. J. Gallagher contributed an account of some work which he has been doing in Professor Büsgen's laboratory on the comparative anatomy of the rootlets of Cupuliferæ and Meliacæ in which he correlated the anatomical characters with the "extensive" or "intensive" function of the rootlets.

The semi-popular lecture was delivered by Professor Yapp who gave an excellent account of the vegetation of different regions of South Africa, illustrated by beautiful lantern slides from his own photographs.

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### EXCURSIONS, ETC.

The local arrangements were under the able direction of Dr. Burt, of the British Botanical Association, who arranged excursions on the Friday, Saturday and Tuesday afternoons to Askham Bog, Castle Howard and Skipwith Common respectively. Askham Bog and Skipwith Common are flat low-lying tracts of land in the alluvial plain of the Ouse, and showed many of the characteristic features of the inland peat formation on the sites of old meres, as well as the development of a heath flora and colonisation by birches and pines in the drier parts. A beautiful feature of Skipwith was the abundance of the marsh Gentian (*G. Pneumonanthe*) in full flower. The zonation of the vegetation in the order, *Juncus*, *Molinia*, *Erica Tetralix*, *Calluna*, within two or three feet of altitude was very sharply marked. *Riccia crystallina* and *Botrydium graucolatum* were discovered close to a pond near the Common. The former plant, we understand, is new to Yorkshire.

On Monday afternoon the members of Section K paid a visit to the grounds and laboratories of the British Botanical Association, on the invitation of Dr. Burt. Tea was provided and the members were photographed in the grounds of Messrs. Backhouse's nurseries. In the evening a successful dinner was held at the Davyhall Restaurant.

Among the guests of Section K were Professor E. C. Jeffrey, of Harvard, and Dr. A. F. Blakeslee from America, Professor Potonié from Germany, Professor Johannsen and Dr. Ostenfeld from Copenhagen, and Dr. Rosenberg from Stockholm; the last three coming particularly for the Discussion on Fertilisation.

THE BOUCHE D'ERQUY IN 1906.

[TEXT-FIGS. 29—31.]

FROM time to time short accounts have appeared in this Journal of the ecological work on halophytes upon which successive expeditions, organised by the Botanical Department of University College London, have been occupied on the Bouche d'Erquy in Brittany.<sup>1</sup>

On the occasion of the first visit (1904), the physical features and salt-marsh vegetation of the estuary were mapped as a preliminary to further study; last year "stations" were located

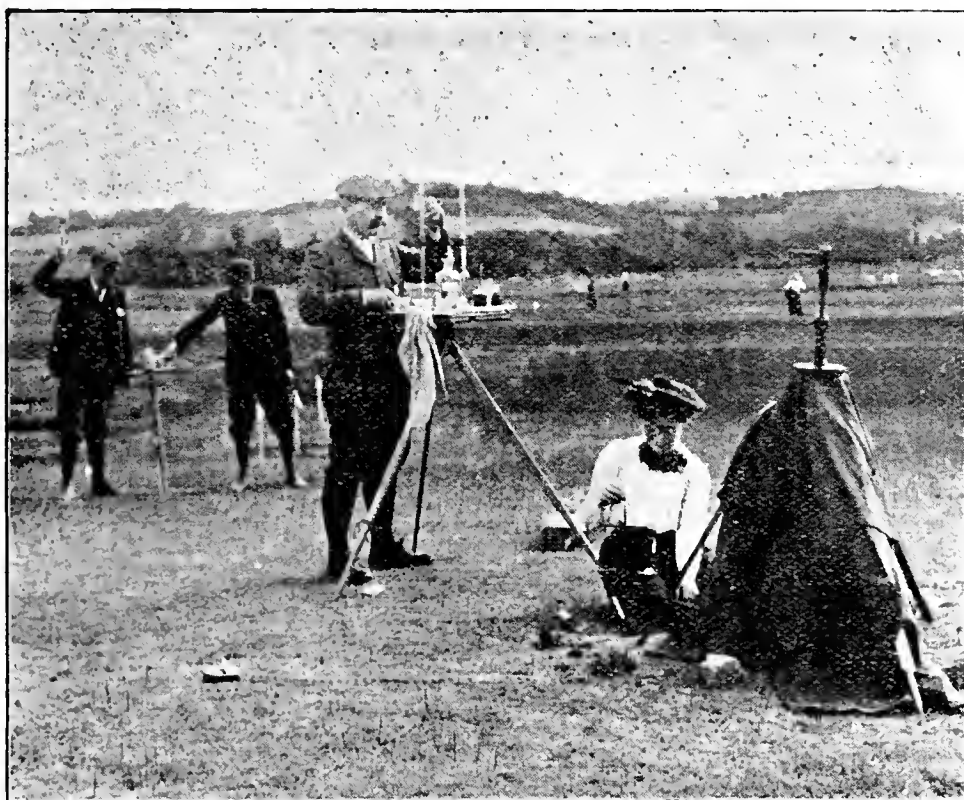


Fig. 29. The Field-Laboratory on the occasion of the first visit in 1904. Soil weighing and salt-determinations are in progress in the foreground: the figures behind are engaged in driving a soil-borer into the earth.

in typical homogenous areas and their vegetation studied by means of the high scale charting methods devised by Dr. F. E. Clements. At the same time periodic determinations were made of the water-contents and salinity of the soils from the different stations, with a view to ascertaining how far the local variations of the vegetation are correlated with physical differences of habitat.

<sup>1</sup> New Phytologist, Vol. III. p. 200; Vol. IV., p. 192.

A visit by two observers was also paid in November last to collect seed for cultural work at home, whilst in April numerous reciprocal transplantations of the seedling *Salicornias* or *Suaedas* were carried out between the different habitats. A further visit was also made in July.

During the autumn of the current year (September 1—15), a party of about twenty persons went out to continue the work. Following the precedent of former years they were organised in sections, each of the seven sections specializing on some particular branch of the investigation.

Section A was entrusted with the continuation of the general map (Scale 1:240) which they extended so as to include certain areas which had been at a former period reclaimed from tidal encroachment, but have reverted to marsh once more, owing to the sea-walls falling into disrepair. The rather peculiar relations of the vegetation in these secondary marshes, will, it is thought, repay more detailed study than they have yet received. These, together with the upper reaches of the estuary, as far as the influence of the tides is felt, were levelled for contouring purposes.

Section B studied the distribution of the Algae and mapped them along the whole course of the main river as it runs through the estuary to the sea. This survey led to the detection of several features of considerable interest relating to the effect of substratum and rate of flow, respectively, upon the algal vegetation. It is hoped that as this part of the investigation is pushed on something may be ascertained of the behaviour of the Algae in regard to the tidal cycles and of the part they play as soil formers.

Section C re-charted the "quadrats" which had been made permanent the previous year. Several additional stations—including two in the secondary marsh—were selected and quadrats charted. The work of this section, taken in connection with the series of charts prepared last year, is very instructive and is now undergoing detailed analysis and tabulation so that the data of the two successive years may be closely compared. Mention may be made of two striking features which this year were apparent to all familiar with the marsh and which are fully recorded by the charting methods employed.

The vegetation as a whole was dwarf and stunted as compared with the corresponding periods of 1904 and 1905 (first fortnight of September). Thus the shoots of *Obione portulacoides*, so conspicuous a feature on the banks of the streams and watercourses in 1904,



stood out this year from the turfy covering hardly at all and had lost all value as a feature in the scenery. The annual *Suaedas* and *Salicornias* in their various forms reached on the average only  $\frac{1}{2}$ — $\frac{1}{3}$  of their usual height. Correlated with this failure to expand, the individual plants, though small, were found to be present in such great numbers as to occasion difficulty in re-charting quadrats on the scale found suitable the preceding year. The numbers in some cases were comparable to those shown by seedlings early in the season before competition for space becomes acute. The explanation is doubtless to be sought in the prolonged drought and

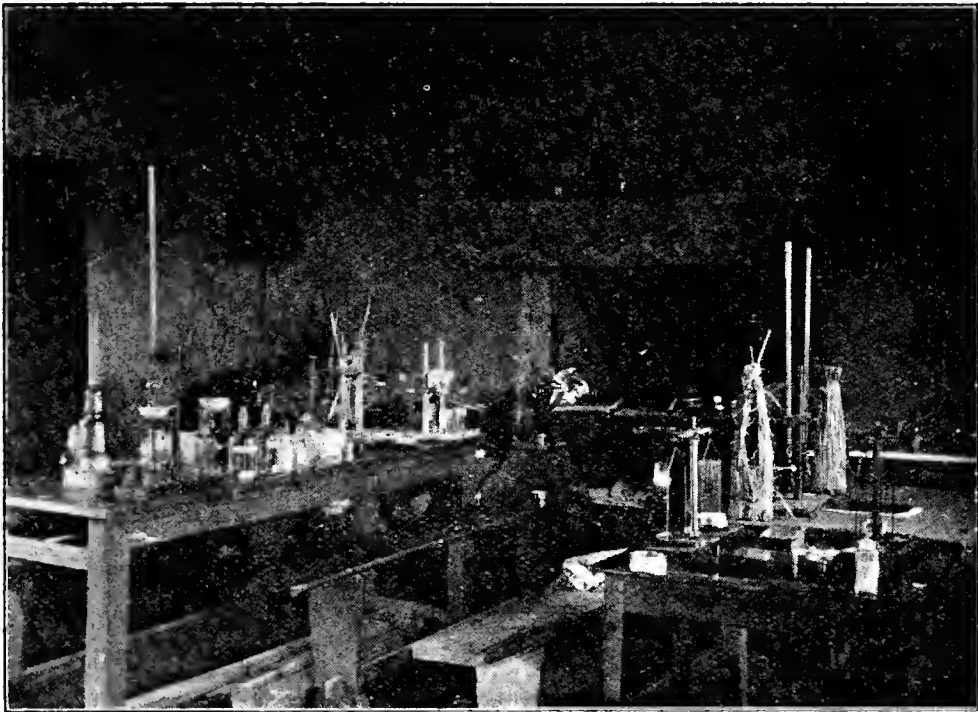


Fig. 30. View inside the Laboratory, with equipment for chemical and physical work (1906).

consequent high soil-salinities that have ruled this year. The daily records of rainfall on the area, taken for us by a local proprietor, shew an average of .6 in. monthly for the three months preceding the visit. Evidently the sea-water, which covers the marsh some twenty times a month, is inadequate to bring the vegetation to its full development—a conclusion which quite accords with the results of several series of cultivations carried out in London on seedling halophytes during May and June.

The other feature of mark was the partial replacement of the “apple-green” *Salicornias* by the crimson type. In explanation it may be mentioned that the surface of the marsh is marked by shallow undulating channels and isolated depressions, which in

1904 bore a fairly pure apple-green type of *Salicornia*. To a slight extent last year, and this year in marked degree, the crimson form ousted the green. So much so that in extreme cases areas previously green had become wholly red.

The work of Section D ("Transplantations and Heredity Problems") dealt largely with the sort of problem exemplified in the last paragraph.

In 1905 about a dozen reciprocal transplantations were made, whilst at Easter this year a very large number of small sods of seedlings were interchanged between the principal habitats. The scrutiny of these and the carrying out of such additional transplantations as gave promise of yielding useful data fell to the lot of this Section.

The object of a transplantation is two-fold. First, there is the direct action of the new habitat upon the plants when they have settled down in their new surroundings; secondly, and perhaps more important, in the event of seed being ripened or dropped, there are the characters shewn by the plants of the next generation. In this way, in two cases of last year's transplantations, the apple-green form of *Salicornia* seemed to have perpetuated its type in the seedlings arising after it had been transferred to two other quite distinct habitats. However, results such as these must be accepted with some reserve, for analysis of the portions of soil that accompany the transplantations shew them to be somewhat retentive of their former properties as regards both the amount and salinity of the water held. It is evident that, as a method, transplantation must be employed with discrimination and should be checked by actual sowing of seeds in appropriate natural or artificial habitats. Several series of dibblings of seedlings which were made in April with this object in view, were, on the whole, a failure, owing to difficulty in effecting establishment. This difficulty may have been aggravated in this instance by the abnormal drought; but, be this as it may, the problem of stability of characters seems best capable of attack by planting the seeds themselves.

The same section gave some attention to studying the mode of pollination of the *Salicornias* and performed a number of crossings—an operation of some difficulty, the success of which remains to be proved.

Section E ("Denudations and Migrations") devoted considerable attention to an investigation of the physical effects of baring the soil, and to a comparison of the vegetation of bare and covered

soils, respectively. The results obtained should pave the way to an elucidation of a number of phenomena relating to plant-growth on the Bouche which have not as yet been the subject of systematic enquiry.

In addition to this, the same Section devised many experiments with a view to tracing the way in which seeds are scattered through the action of the tides. Direct observation of seed-dispersal being possible only in winter, recourse was had to the indirect method of



Fig. 31. Outside the Laboratory : osmotic determinations in progress (1906). denuding suitable areas of some one plant or of its whole covering of vegetation. By noting next year the number and position of the new plants on these areas it should be possible to draw conclusions as to the relation which the general seed-dispersal holds to the mere dropping of seeds at the base of the parent.

Sections F and G, concerned with physiological and chemical work, respectively, had as head-quarters the laboratory installed last year in the main room of an empty cottage by the border of the marsh.

The Physiological Section concentrated its attention upon osmotic determinations of the cell-sap of the halophytes and upon the influence of soil factors upon absorption and transpiration.

In the absence of previous experience at Erquy the time available proved all too short to test thoroughly the value and appropriateness of different methods in osmosis when applied to halophytes. Speaking quite generally the osmotic pressures were determined by plasmolysis and were found to rule high as compared with ordinary land-plants,—a result fully confirmed when Barger's capillary tube method was employed. Whilst between allied species or forms of halophytes, as such, constant differences in osmotic pressure do not appear to hold, there is considerable reason for suspecting the reverse to be the case with plants from habitats characterised by differing salinities. On the strength of these indications, therefore, importance attaches to the habitat as the determining factor in sap-concentration. In the light of the experience gained a full trial will be possible on a future occasion.

The Chemical Section continued the work of last year upon the amount and salinity of the water in the soils from the different stations and also made several partial analyses of plants of differing habitat. In view of the prolonged drought and consequent high evaporation it was not surprising to find the soil-water salinities ruling much higher than was the case last year. In some cases the variations in salt-content corresponded with differences in the vegetation.

Regarding the salt contained in the plants themselves, in the cases investigated its amount followed generally the salinity of the habitat.

A few sugar estimations were made but they did not confirm the conjecture that the red forms would prove richer in sugar than the green. The question of colour in halophytes is very interesting and attractive, but depends on some subtle combination of factors, the nature of which has not yet been reached.

With the experience of previous years to guide and the great convenience of the cottage for the secure storage of apparatus of all kinds, organisation was rendered easy. Whilst each section had its duties broadly defined in advance so far as the problems with which it had to grapple are concerned, there was a considerable margin left to individual initiative—an initiative usefully displayed on many occasions during the progress of the work.

Whether as a scientific investigation or a means of training it is of importance not to risk stereotyping field-work of this kind by a too rigid adherence to the details of a set plan of operations.

It only remains to say that as on former occasions the party met with every courtesy, alike from the inhabitants and local officials.

F.W.O.

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## BOTANY FOR YOUNG PEOPLE.

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The Study of Plant Life for Young People, by M. C. Stopes, D.Sc., Ph.D., Assistant Lecturer and Demonstrator of Botany at the University of Manchester. pp. XII. and 202. With numerous illustrations. London, Alexander Moring, Limited; the De La More Press, 32, George Street, Hanover Square, W., 1906.

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IN her preface, the author of this little book reminds us that “*learning* rather than teaching, is the essential factor in education,” and her attempt to provide “a guide along the road for those who desire to learn something about the plants around them” may be unhesitatingly pronounced a great success.

A great feature of the book is the placing of the main facts of “The Life of the Plant,” as determined by simple physiological experiments in the forefront. The first fifty pages are devoted for this exposition, so that a logical and connected idea of the life work of plants is gradually built up before any of the special phenomena which occupy most of our elementary botany courses are touched on. Part II. is devoted to “The Parts of a Plant’s Body, and their Uses.” Part III. to specialisation for protection against loss of water, for climbing, etc. Part IV. to “The Five Great Classes of Plants,” and Part V. to “Plants in their Homes.” The resolute facing at the outset of the fundamental principles of plant life, immensely simplifies the author’s task in later chapters.

Perhaps the most original and striking part of the book is the concluding section on “Plants in their Homes,” which appeals to the reviewer as written with a breadth and knowledge he has not met before in an English elementary work. It is admirably led up to

by the preceding sections and there is just enough information and suggestion to stimulate interest along the best lines.

Of fault finding, we have extraordinarily little to do. The book is written in a bright colloquial style, for the most part pleasant and easy, but the English is not always beyond reproach, and some of the sentences are very clumsy. A little more care in proof correcting would have removed this blemish.

We do not agree with the author that the microscope should be wholly excluded from the work of children. It is obviously true that a detailed course of histology is quite out of place, but it is most desirable that the young student should learn the main facts about cells from personal observation, and the peep into this new world if rightly subordinated to the whole work, is in itself a fascinating experience, justifiable on all grounds. Craven fear of the microscope is as weak as slavish devotion to it.

The illustrations consist of a number of line drawings, mostly adequate and good, done specially by the author for this book, and some well chosen half-tone blocks of "plants at home," two or three of which are admirable. Fig. 148 we imagine, represents *Salicornia herbacea*. It is better to use the ordinary English name of this plant—Glasswort, rather than "Marsh Samphire," to avoid confusion with the Samphire (*Crithmum maritimum*), quite a different plant, with functional leaves, and characteristically growing in rock clefts, above high tide-mark.

The book is very well got up, has large clear type and a pretty and useful green cover. It cannot fail to be helpful even to the good modern school teacher, and we cordially wish it a large circulation.

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We have received a little paper-covered book called "Toadstools at Home," by Mr. Somerville Hastings. It is one of "Gowan's Nature Books" and costs sixpence. The book consists of sixty excellent half-tone reproductions of photographs of British Agarics and some others of the larger Fungi, with a few pages of information as to what mushrooms and toadstools are and short descriptions of the species figured. The photographs can scarcely be praised too highly and though, of course, representations of these plants necessarily lose a great deal from the absence of colour, the pictures will in most cases suffice for recognition of the different kinds. The letterpress is attractively written, though the print is very small.

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LECTURES ON THE PHYSIOLOGY OF MOVEMENT  
IN PLANTS.

BY FRANCIS DARWIN.

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I.—ASSOCIATED STIMULI.

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I SHALL begin my Lectures on Plant-Movement with a general discussion on the reaction of plants to Stimulus.

The first clear statement of the present point of view occurs in that often quoted passage in Dutrochet<sup>1</sup> in which he declares that the movements are "spontaneous," being executed "à l'occasion de l'influence d'un agent extérieur, et non des mouvements imprimés par cet agent." A discussion of the meaning of the word *spontaneous* would lead us too far. On the other hand, if we deny to living organisms what is commonly known as spontaneity, we are driven to adopt automatonism.

No doubt if we take a severely logical view of the universe with Descartes, we may be obliged to admit that our actions are the direct inevitable result of what has previously occurred in the world, and that we are forced into a certain action just as inevitably as the mercury in a thermometer is forced to rise to a certain point. But this is a point of view which leads us no further, it is not an instrument of research. To get a point of view which is physiologically valuable we must retain the idea of spontaneity. What we do at a particular juncture depends on the nature of our previous experiences and actions. The "self" which seems to be spontaneous is the balance which weighs conflicting influences.

<sup>1</sup> Quoted by Pfeffer from Dutrochet, *Recherches anat. sur la Structure, &c.*, 1824, p. 107.

It is for this reason that even in plant physiology we want the idea of a individuality, a something on which the past experience of the race is written and in which the influences of the external world are weighed. I do not of course imply conscious weighing, nor do I mean that the plant has memory in the sense that we have memory. But a plant has memory in Hering's and S. Butler's sense of the word, according to which memory and inheritance are different aspects of the same quality of living things. Thus in the movements of plants, as in the instincts of animals, the spontaneity of the individual has disappeared, the balance of profit and loss has been struck during the past experience of the species, and the individual acts by that unconscious memory we call inheritance.

My view of the nature of stimulus and reply depends on what in mental processes is known as association. The smell of a flower or the recurrence of a bar of music may act on a man as a stimulus in virtue of their association with events in his past life. I want to be able to talk about association without connoting mental processes and I shall therefore devote a short time to a remarkable book "Die Mneme" by R. Semon, in which a terminology has been framed, which is equally applicable to the movements of a plant or the thoughts of a man.

Semon contrasts the behaviour of a puppy who takes no notice of a boy stooping to pick up a stone with that of an adult dog (experienced in the ways of boys) who runs when he sees the stone picked up.

When the puppy has for the first time been hit by a stone, he receives two stimuli, *viz* : the image of the boy on his retina and the pain from the blow of the stone. The result is that the organism is permanently changed; before, the stone-throwing produced no perceptible effect, while the pain caused him to run. Afterwards the effect of running away can be produced by the retinal stimulus. The permanent change in the organism he calls an *engram* or record, something written or engraved on the organism. Thus the image of the boy gives the engram I. the pain of engram P. Two engrams occurring together (or in close succession) tend to be tied together. Thus when the dog again sees a stooping boy the engram I. is called up and brings with it P., to which it is united. In this case the result (the running away) is *ecphorically* produced, which I imagine to mean a dragging out or revival of one engram by another. The whole process he calls *mnemic*—not that it implies



memory in the sense of conscious reminiscence, but simply the recall of a previous condition of the organism. It must be noted that on the second occasion, when the dog runs at the sight of the boy stooping, there is repetition of the direct stimulus and also an awakening of the engram I., so that there is co-phory of I., as well of of its associated engram P. We may imagine at a third or fourth repetition of the stone-throwing experience that the image of a boy—a good boy who has no intention of picking up a stone, will be sufficient to act as a stimulus. That is to say a small part of the original stimulus, will revive the whole of the now deeply engraved engrams I. and P., and as before the dog will run.

These cases are of interest because they seem to indicate a way in which organisms can become more sensitive to any stimulus by its repetition. It is of importance to an organism which has to exist in a complex and hostile environment that it should be highly sensitive to external change, and especially that it should perceive a coming danger before it has reached a hurtful intensity. No doubt this heightened sensitiveness is selected like other adaptations. But we see here that without the existence of variation in sensitiveness there is in the mnemonic capacity a possibility of automatic increase of sensitiveness.

An instance of associated engrams occurs in the reactions of the gemmæ of *Marchantia*, investigated by Pfeffer.<sup>1</sup> The gemma has dotted over its surface certain cells, some of which finally develop into rhizoids. The question which shall so develop is settled by at least two factors—sensitiveness to gravity and to contact<sup>2</sup>.

In the ordinary course of events the gemma falls on the ground and the root-hairs grow on the physically lower surface. This surface is also that on which contact occurs. In Pfeffer's experiments the gemmæ were fixed to the roof of a damp chamber, roots appeared on both upper and lower surfaces.

We may suppose that the contact-irritability and the gravitational sensitiveness may have been independently evolved. But the point I wish to make is that if one of these qualities were developed the other would follow by association of engrams. If for instance the root-hairs were originally developed exclusively in response to gravity, *i.e.*, on the physically lower side, the growth of the hairs would be accompanied in the majority of cases by contact on the

<sup>1</sup> Sach's Arbeiten, I., 77.

<sup>2</sup> Benecke, B.Z., 1906, doubts whether the stimulus is actually contact. It seems probable that the reaction depends on the presence of water containing salts in solution.

lower side. The engrams of gravity and contact would be associated and contact would produce the result originally due only to gravity. In this way a plant manufactures its own stimulus—or as it may be expressed, discovers accessory guides.

Another example of association may be taken from the germination of a *Cucurbita* seed.<sup>1</sup> The lateral process or peg grows on the physically lower side of the radicle at the junction of the root and hypocotyl. The hypocotyl is oval in section, its longer diameter being parallel to the plane of the cotyledons. In the great majority of cases the flat seeds of the *Cucurbita* must lie on the ground with the plane of the cotyledons horizontal. Therefore in the majority of cases the peg must develop on one of the flat sides of the radicle. Now imagine a seed sown on its edge with the radicle horizontal as before but with the plane of the cotyledons vertical. The peg will grow on the lower of the two edges of the radicle; but what is remarkable is that an outgrowth also occurs on both the flat sides.

The same sort of thing occurs when the seed is sown vertically. Here we imagine that since gravity cannot settle on which surface the peg shall appear, it grows on both sides. In both these instances, the growth of the peg on the flat sides of the radicle may be conceived to have become associated with the early stages of germination; so that these stages cannot occur without the result following. These cases seem to me difficult to fit into the modern point of view according to which a plant is compared to a substance possessing certain properties. According to this view, the property of a *Cucurbita* seedling is to produce a peg on the physically lower surface of its radicle. But to account for all the circumstances we must assume that it also has the physical property of producing out-growths on the flat sides of the hypocotyl, when the seed is vertical. No doubt one assumption is as easily made as the other. But the two assumptions are isolated and sterile. Whereas by bringing in the principle of association we might almost have prophesied what would take place. I shall return to the *Cucurbita* seedling later, for its peg is an excellent object on which to hang discussions of this character.

Some interesting examples occur in a paper by Massart.<sup>2</sup> In describing the germination of the bulb of *Ornithogalum* he mentions (p. 52) that the leaves are parallel as they make their

<sup>1</sup> Noll, Landw. Jahrb. XXX.

<sup>2</sup> Bull. Jardin Bot. Bruxelles, 1903.

way out of the ground, and that they curve outwards and separate on emerging into the light, *i.e.*, that light produces epinastic growth. In the tulip, *T. gesneriana*, the spreading out of the leaves which normally occurs in the light, occurs after a time even in darkness. Massart points out by the help of other examples, that a series can be shown to exist between *Ornithogalum* and Tulip, in which the action of internal stimulation increases.

Cases like this, in which an action normally occurring as a response to a definite stimulus takes place without the stimulus, are familiar among periodic phenomena, for instance in the well-known case of sleeping plants continuing for a time their rhythmic movement in darkness.

The phenomena of etiolation are interesting in relation to our view of stimulus. Many writers fail to see that the phenomena are of the same nature as more obvious cases of reaction to stimulus, and treat them as isolated pathological facts. A seed buried in the ground begins its life in darkness and normally completes its development when it emerges under the changed conditions of illumination. So that if it cannot reach the light, it is suffering from the absence of a normal stimulus. And since from a biological standpoint, accidentally prolonged darkness is a normal occasional event in a plant's life, we should expect adaptations to these conditions.

Such adaptations do, I believe, occur; in any case it seems to me futile to attempt to "explain" a complex set of facts as due to disturbed nutrition. In human beings, malnutrition of children produces rickets, but the deformity has no tendency to help the child to escape from the conditions and is not adaptive. But in plants the results, as a whole, are clearly adaptive.<sup>1</sup>

The plant throws its whole energy into elongation, and this growth takes place in the parts of the plants which are best adapted to escape. In ordinary Dicotyledons we find exaggerated growth of the internodes with dwarfing of the leaves, in Cereals and in other Monocotyledons, such as Crocus and Hyacinth, great elongation of the leaves. This is easily comprehensible as an adaptation, but not as a direct result of malnutrition. Why should want of food make a Crocus leaf at the same time long and abnormally narrow? Nor does the direct result of malnutrition explain why for instance a Narcissus scape should be greatly elongated in the dark. From

<sup>1</sup> See Godlewski, *Biolog. Centralblatt*, 1899, and F. Darwin, *Journal R. Hort. Soc.*, Vol. XIX.

my point of view, it is clear that to the Narcissus flower-stalk, light is a signal that it has reached the open air, where alone its flower is capable of normal action. The same point of view is applicable to *Coprinus*: the stalk grows enormously, even as much as two feet in length, while the cap is either dwarfed or absent. Here again light is the signal that the cap has reached the open air where the spores can advantageously be scattered.

It is instructive—and very much against the malnutrition theory, that the morphological peculiarities of etiolated plants appear where there is no malnutrition. According to Sachs the Hop is not affected by darkness, because it is “naturally etiolated” *i.e.* it is already throwing its whole energy into exaggerated longitudinal growth as an adaptation to the climbing habit. In the same way Noll<sup>1</sup> proposes to apply the term etiolation to the exaggerated growth of the petioles of certain floating leaves when the level of the water is artificially raised.<sup>2</sup>

To return to etiolation in the usual meaning of the word. Although I deny that the direct action of malnutrition explains the facts, yet as a stimulus it must be reckoned with. The condition of the plant which shows itself outwardly in elongation of internode and dwarfing of leaf is associated with darkness and with a certain degree of starvation. When the plant emerges from darkness, it is subject to two new conditions, *viz.*—illumination and a state of healthy nutrition due to assimilation. We have seen that the result normally due to two stimuli may be produced by one of them acting alone. Therefore we ought perhaps to find, if the plant is supplied with sufficient food, that etiolation will cease even in the dark.

This has been shown by Jost to be the case (Pringsheim's Jahrb. XXVII, p. 444). A single leaf, nourished by the illuminated part of the plant, develops normally in complete darkness if freed from competition by the removal of all buds. Again Benecke (*loc. cit.*) shows that the gemmæ of *Lunularia*, which normally refuse to germinate in darkness will do so if supplied with sugar in solution.

On the other hand Vines found that some plants starved by

<sup>1</sup> Sitz. Niederrhein. Ges. f. Natur- u. Heilkunde z. Bonn, 1901.

<sup>2</sup> Benecke (Bot. Zeitung, 1906), speaks of the etiolation of the rhizoids of *Lunularia*, the exaggerated longitudinal growth being here produced by starving them in the matter of nitrogen.

exposure to light in the absence of  $\text{CO}_2$  are not etiolated,<sup>1</sup> here the stimulus of light is enough without the stimulus of nutrition.

I am inclined to think that a form of etiolation produced by damp air is a case of associated engrams. Certain rosette-leaved plants do not retain their characteristic form in darkness, but spindle out into a shoot, and in some—not all—of these, the same effect may be brought about by exposing them to damp air in light.<sup>2</sup> This must, I think, depend on the fact that dampness and darkness occur together in nature, *e.g.* under ground, and in a less marked degree under heaps of dead leaves or other debris. The occurrence of this form of etiolation is capricious, thus *Plantago* gives no such reaction, *Sempervivum* reacts to both darkness and damp air, *Capsella* to damp air but not to darkness.

Finally, I must add, that I do not pretend to be able to explain the whole of the facts of etiolation, which have only been introduced to illustrate a possible case of associated engrams.

The association of stimuli accounts, as Semon suggests, for many of the curious cases known as change in “*Stimmung*” *i.e.* disposition or tone.

The spores of certain Ferns do not normally germinate in darkness,<sup>3</sup> but by a temperature of  $32^\circ\text{C}$  they can be made to germinate in the dark. To say that these are cases of change in tone is to re-state the fact in other words, but if we may look on them as due to associated engrams we at least classify them with a large group of phenomena.

I should suppose that light and warmth generally occur together, and that an act carried out at the suggestion of illumination would generally occur simultaneously with raised temperature. Therefore the engrams of heat and light would come to be associated, and accordingly it is conceivable that heat alone should produce the effect normally due to light and heat.

In considering the periodic movements of sleeping plants, we shall see that there is some evidence of heat producing the effect normally due to light.

I have a few words to say on the adaptive character of plant reactions. Even those who look on adaptation as an abomination of desolation, standing where it ought not, cannot deny the fact that the outcome of reactions to stimuli is, broadly speaking,

<sup>1</sup> In other cases serious disturbances to growth are produced by these conditions.

<sup>2</sup> Wiesner, *Ber. Deutsch. Bot. Ges.* IX., 1891.

<sup>3</sup> Pfeffer's *Physiologie*, II., p. 105.

beneficial. But it is also clear that there are a number of cases of stimulation which are not adaptive. The most striking are those in which a plant reacts to an agent which does not occur in nature.

Take for instance the widely spread reaction to electric shock. Here we can only say that there is a rough resemblance between electric disturbance and other destructive agents to which the organism is normally adapted. The resemblance between a natural and unnatural agent undoubtedly accounts for some phenomena. Thus the spermatozoa of ferns are adaptively attracted by malic acid, but they are also attracted by maleic acid which does not occur in nature.<sup>1</sup> Here the chemical relationship of the two substances may account for their identical reaction. But how are we to account for Buller's<sup>2</sup> experiments in which it was shown that relatively strong solutions of several salts also attract? Rothert<sup>3</sup> points out that the attraction of bacteria by ether can hardly be explained in this way. On the other hand as Pfeffer<sup>4</sup> apparently allows, the fact that bacteria are attracted by rubidium salts may be accounted for by their resemblance to those of potassium, which commonly occur in nature.

On the whole it may be said that there is nothing fatal to our point of view in the fact of a highly labile structure reacting to a cause to which it is not adapted.

I do not mean to minimise the difficulty, but in fairness it must, *per contra*, be allowed that there are many cases in which organisms fail to react to non-natural causes. Take for instance the well known case of spermatozoa being lured to their death by a mixture of malic acid and corrosive sublimate or other poison, no capacity for perceiving the presence of these poisons having been evolved.

In other cases the supposed reaction to non-natural causes are ascribable to faulty observation. Thus the whole case for galvanotropism falls away before the observations of Bayliss and Ewart<sup>5</sup> who have shown that the curvatures are simply due to chemotropic reaction to the substances produced at the electrodes. Again it is not impossible that rheotropism, the reaction to flowing water, may turn out to be a case of sensitiveness to pressure. If so it

<sup>1</sup> Pfeffer, Unters. Bot. Institut., Tübingen, I.

<sup>2</sup> Annals Bot. XIV., 1900.

<sup>3</sup> Flora, 1901, p. 382.

<sup>4</sup> Unters. Bot. Institut., Tübingen, II., p. 649.

<sup>5</sup> Proc. R. Soc., B. 514. 1905.

would pass from the category of non-adaptive phenomena to one where at any rate adaptation is more possible.

In all cases of adaptation we must (as my father said) be constantly on our guard against assuming, because we do not recognize a function, that no function exists. I personally prefer an excess of imagination to defect in that respect. I welcome the theories of that imaginative botanist, Stahl, though I may not agree with all of them.

As a small instance of the use of scientific imagination may be mentioned an idea of Rothert.<sup>1</sup> He quotes Jennings as expressing surprise that *Paramœcium* should be attracted by  $\text{CO}_2$  "since it is very improbable that  $\text{CO}_2$  should be in any way useful to it." But Rothert acutely suggests that as *Paramœcium* lives on Bacteria, a large assembly of its natural prey would be discoverable by *Paramœcium* following to its source the diffusion of  $\text{CO}_2$ .

The attraction<sup>2</sup> of *Chromatium Weisii* by  $\text{H}_2\text{S}$  would, in the absence of Winogradsky's observations on sulphur-bacteria,<sup>3</sup> have appeared a meaningless reaction, for it is unlikely that anyone would have had imagination enough to guess that these organisms depend on the oxidation of  $\text{H}_2\text{S}$  for a source of energy.

Again the phototaxis of the spores of *Chytridium vorax* would seem to be devoid of adaptation if we did not know that phototaxis helps them to track out their victims, which in their turn follow the light because they are dependent on photosynthesis.

In conclusion I would say that I am well aware that the principle of associated engrams, and the question of adaptation in regard to stimuli require a much fuller discussion than I have been able to put before you.

<sup>1</sup> Flora, 1901, p. 402. Note 2.

<sup>2</sup> Miyoshi, Journal of Coll. of Science, Tokyo, X. 1897, p. 160.

<sup>3</sup> Bot. Zeitung, 1887.

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ON SECONDARY THICKENING IN RECENT  
PTERIDOPHYTA.

## A RÉSUMÉ.

**O**F late years evidence of the presence of secondary thickening in recent Pteridophyta has accumulated, and it does not appear altogether undesirable to gather the recorded facts together.

In investigating secondary thickening in the plants of a family where the process does not usually obtain, some care has to be exercised in determining whether the elements which appear to be secondary in origin, really are so, and are not instances of a slow passage of elements derived from the apical meristem into permanent tissue. Of course, in those cases where a well-defined cambium is developed, this danger does not exist; a cambium, however, is not always present, hence the need for caution.

To take a possible example; immature elements might be found in relatively old parts of a member, and may or may not be secondary. To determine whether they are of secondary origin or not, evidence of tangential divisions are to be sought for, and careful comparison made with the structure obtaining in the younger parts of the same member, where the tissues are still in a more or less meristematic condition. If no evidence of such a division can be found in any of the regions of the older parts under consideration, then the case would be what has been described above as a slow passage of elements, derived from the apical meristem, into permanent tissue.

It is almost unnecessary to say that in all the instances of secondary thickening considered below, the requisite care has been exercised, and, in the mind of the present writer, there is no doubt that the records are those of true secondary thickening, although often of a very rudimentary nature.

In the majority of cases, xylem is the chief secondary product, and the later-formed elements of this tissue may be distinguished by the following means:—

(i.) *Position.* The secondary elements of the wood are usually situated on the outside of the primary xylem, and in the older parts of the plants. The age of the member is of importance, and can be more or less accurately determined by the number of roots or of leaves, in the case of a stem for example; and by the habits of the plant, more especially whether it be slow-growing or not.



## *On Secondary Thickening in Pteridophyta.* 209

(ii.) *Appearance.* The secondary tracheides are often of somewhat slow development, and in many cases there may be seen immature elements with their walls partially lignified and still retaining living contents.

(iii.) *Relation to adjacent tissues.* There may be seen a more or less definite seriation, the elements appearing in radial rows. This character must, however, be used with caution, for the cells of the primary tissues may sometimes exhibit a radial arrangement.

### OPHIOGLOSSACEÆ.

#### *Literature.*

Boodle.—On Some Points in the Anatomy of the Ophioglossæ.  
Ann. Bot., Vol. XIII., 1899.

Russow,—Vergl. Untersuchungen. Mém. de l'Acad. imp. des  
Sciences de St. Pétersbourg. Sér 7, t. XIX., 1872.

### BOTRYCHIUM LUNARIA.

*Stem.* The presence of cambium, and its activity in the rhizome of this plant, is so well-known that nothing more than the briefest description is necessary. It is sufficient to observe that the cambium occurs in a normal position between the primary wood and the phloem, and constantly adds new elements to these two tissues. The process is thus of a type characteristic of a normal Dicotyledon or Gymnosperm.

*Root.* Boodle has shown that there is a considerable addition of secondary tracheides in the bases of the roots, more especially in those regions which are embedded in the cortex of the rhizome. The characters of this later formation of new tissue is of the same nature as that of *Ophioglossum* described below.

### OPHIOGLOSSUM VULGATUM.

*Stem.* An addition of secondary tracheides takes place on the outer margin of the primary wood of the older parts of the rhizome, and it is to be observed that there is no definite cambium. The later-formed elements may be recognized by their reactions with certain stains (see Boodle, *loc cit.*)

*Root.* The phenomenon in question is similar to that which obtains in the rhizome, but the addition of tracheides takes place on all sides of the xylem, and not merely on the outer margin as in the stem. As before, there is no cambium; there may, however, sometimes be made out a radial arrangement of the new elements; but, as has been pointed out above, this feature is not to be absolutely relied upon in determining which elements are primary and which are of secondary origin.

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The greatest addition of new tracheides is to be found in the bases of the roots, which fact corresponds with what has been found to obtain in the roots of *Botrychium*.

### MARATTIACEÆ.

#### *Literature.*

Farmer, J. B., and Hill, T.G.—On the Arrangement and Structure of the Vascular Strands in *Angiopteris evecta* and some other Marattiaceæ. *Ann. Bot.*, Vol. XVI., 1902.

Hill, T. G.—On secondary Thickening in *Angiopteris evecta*. *Ann. Bot.*, Vol. XVI., 1902.

### ANGIOPTERIS EVECTA.

*Stem.* The secondary thickening which occurs in this plant, is of a somewhat more definite nature than what obtains in the *Ophioglossaceæ*, for there is a fairly well-defined cambium formed by the division of the parenchymatous tissue surrounding the xylem. These merismatic cells do not extend around the whole of a vascular strand, but are local in their occurrence; in the best examples, from six to eight such elements may be observed. The amount of xylem produced is small, being rarely of more than three cells in depth and this only in the best instances; the more usual thing to find is the occurrence of single tracheides.

Besides this intrastelar secondary tissue-formation, there is also a very regular cambial division in the endodermal layer. This activity leads to the formation of sometimes as many as six layers of cells arranged in a radial manner; the products of the division remain parenchymatous, but the outermost elements may faintly respond to the test for endodermis.

*Leaf.* Occasionally there may be seen secondary tracheides bordering the xylem of the leaf-trace at the base of the petiole. No cambium has been observed, there is merely an addition of single elements.

*Root.* No observations regarding secondary thickening have been recorded.

### MARATTIA FRAXINEA.

*Stem.* The process is of exactly the same nature as has been described for *Angiopteris*. There is also, in *Marattia*, the same thickening of the parenchyma bordering on the stele, but not to so great an extent as in *Angiopteris*.

As regards the other members of the Marattiaceæ, no addition of secondary elements seemingly takes place in *Archangiopteris*, *Danaea* or *Kaulfussia*.

EQUISETACEÆ.

*Literature.*

Cormack.—On a Cambial Development in Equisetum. Ann. Bot., Vol. VII., 1893.

EQUISETUM MAXIMUM.

*Stem.* The examination of a transverse section through a mature node shows that the xylem of the bundles is relatively very extensive, and that the elements of the wood and of the phloem, in the central region of the strand, are arranged in radial rows. This regular seriation is not obvious in the tracheides nearer the centre of the axis nor in the more peripheral phloem-elements, in fact "the whole arrangement suggests that a plate of tissue has been intercalated between two older growths by the activity of a cambium-like meristem." The opinion here expressed is strengthened by the examination of tangential and radial longitudinal sections, from which it is seen that the characters of the elements interposed between the xylem and phloem are those usually associated with a normal cambium; and further, the formation of new cells is similar to that obtaining in ordinary secondary thickening.

Corroboration is to be obtained by the comparison of sections of stems of different ages. By this means it is found that the number of elements in the radial thickness of a bundle is about equal both in a young and an old internode. Thus in this region the tangential division is arrested very early. This, however, is not the case at the nodes; the immature node has fewer elements in the radial thickness of a bundle than has the mature node.

Cormack's conclusion is "that after the bundle has attained in the internode its full number of cells in radial thickness, and after tangential division in the corresponding tissues of the node has ceased, a plate of tissue has been intercalated between the protoxylem and protophloem of the node; that the xylem thus formed is mostly reticulately thickened, whereas the thickening of the protoxylem is annular; and that the intercalation has been accomplished by the activity of a meristem whose cells are cambiform."

PSILOTACEÆ.

*Literature.*

Boodle.—Secondary Tracheides in Psilotum. New Phytologist, Vol. III., 1904.

Boodle.—On the Occurrence of Secondary Xylem in Psilotum, Ann. Bot., Vol. XVIII., 1904.

Ford.—The Anatomy of Psilotum triquetrum. Ann. Bot., Vol. XVIII., 1904.

## PSILOTUM TRIQUETRUM.

*Stem.* The formation of secondary xylem elements takes place in much the same manner as in *Ophioglossum* and they occur in the subterranean and aerial axes. No definite cambium is present, but it is possible, in some cases, to make out a radial seriation in the tracheides and the adjoining parenchymatous cells. The new tracheides are sometimes pitted in an irregular manner, but more often the pits are of the normal scalariform type. The secondary xylem elements are situated between the primary wood and the phloem, and, generally, are separated from the former by at least one row of parenchymatous elements. On the other hand they may be in direct contact with the central xylem-mass, and in great part they replace the zone of parenchyma which, in younger axes, occurs between the primary xylem and the phloem.

The examination of longitudinal sections demonstrates that these secondary tracheides pursue a sinuous course, which fact is probably due to sliding-growth.

Boodle, who was the first to discover these tracheides in *Psilotum*, supposes that their formation depends on the development of the aerial shoots, "and appears to be due to a basipetal stimulus from the latter."

## TMESIPTERIS.

So far as the published accounts go, *Tmesipteris* does not exhibit any secondary thickening; it would not be at all surprising, however, to find secondary tracheides in the axes of this plant, provided material sufficiently old were examined.

## SELAGINELLACEÆ.

*Literature.*

Bruchmann.—Untersuchungen über Selaginella spinulosa. Gotha, 1897.

## SELAGINELLA SPINULOSA.

*Stem.* This is the only known species of *Selaginella* which shows the feature under consideration. At the base of the stem, which is a permanent structure, there is an indefinite growth in thickness. The phenomenon is very similar to what occurs in the same region of *Isoetes Hystrix*, but with this difference, that whereas in the last-named plant there is an addition of secondary parenchyma only, in the case of *Selaginella spinulosa* the later-formed elements consist of parenchyma and xylem.

ISOETACEAE.

*Literature.*

Von Mohl.—Ueber den Bau des Stammes von *Isoetes lacustris*.  
Vermischte Schriften. Linnæa, 1840.

Hofmeister.—Beiträge zur Kenntniss der Gefäss-Kryptogamen.  
I. Die Entwicklungsgeschichte der *Isoetes lacustris*. Abhand.  
der K. Sächs, Ges. d. Wissensch., IV., 1852.

Russow.—Vergleichende Untersuchungen, St. Pétersbourg, 1872.

Hegelmaier.—Zur Kenntniss einiger Lycopodien. Bot. Ztg, 1874.

Farmer.—On *Isoetes lacustris*. Ann. Bot., Vol. V., 1891.

Smith, R. Wilson.—The Structure and Development of the  
Sporophylls and Sporangia of *Isoetes*. Bot. Gaz., Vol.  
XXIX., 1900.

Scott and Hill.—The Structure of *Isoetes Hystrix*. Ann. Bot.,  
Vol. XIV., 1900.

ISOETES ECHINOSPORA, I ENGELMANNI, AND I. LACUSTRIS.

*Stem.* The cambium arises comparatively early, about the year after germination in the case of *I. lacustris*, in the parenchymatous tissue surrounding the axial strand. The divisions extend around and above the central cylinder, but not so far upwards as the youngest leaf-trace. The products of the cambial activity are parenchyma towards the periphery and elements of the so-called prismatic zone towards the centre.

The amount of secondary xylem produced is always very small, and sometimes may be quite absent, a fact not surprising in in these aquatic plants.

ISOETES HYSTRIX.

*Stem.* As is well known the cambium in this and the other species examined is a well-marked tissue and arises very early in the life of the plant. There is a certain amount of variation in its position. In some cases it is situated in the tissue immediately towards the exterior of the primary xylem and between the wood and the phloem, in which case it may form new wood, the elements of which directly abut on the tracheides of the primary xylem. This activity however does not last very long, for a new merismatic zone arises further out towards the periphery of the stem. This new cambium forms secondary parenchyma towards the exterior while, on its inner side, it gives rise to parenchyma, phloem and a variable amount of xylem. The anomaly to be observed here is the formation of centrifugal phloem.

This succession of cambial zones is not of general occurrence ; in the majority of instances the merismatic zone last considered is the only one produced, and it remains active throughout the whole period of secondary growth in thickness.

A few cases have been described in which there was produced a new cambium internal to the first. In these cases the new meristem arise in the parenchyma—secondary in origin—a little towards the exterior of the primary xylem. This cambium behaves in a precisely similar fashion to the pre-existing one, giving origin to new parenchyma, phloem and wood on its inner side.

It is obvious that the secondary thickening is, in this plant, very variable. Taking its most constant features, as regards the locality of the cambium and the direction of formation of its secondary products, as the normal, it is more like the process obtaining in *Dracaena*, a fact pointed out by the earlier observers.

The amount of secondary xylem produced is very variable; these tracheides are always present however and they agree in all essentials with the lignified elements of the primary wood.

There remains to be mentioned the slow downward growth of the stem, a feature which has been made much of in the past. This downward growth is due to the activity of the cambium, which at the base of the stem appears to form parenchyma only. This is a point of some importance and shows that there is no real homology with the apical growth of a primary root.

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It is not proposed to enter into any elaborate discussion regarding the significance of the presence of secondary thickening these plants. Attention, however, may be drawn to the opinion that, on the whole, the recent Pteridophyta exhibit considerable reduction. A large number of the fossil Pteridophyta possessed marked powers of secondary growth in thickness, and therefore it is not a matter for surprise to find that certain of their descendants still retain traces, more or less well-marked, of this capability. For example the obvious connexion between *Equisetum* and *Calamites* may be cited.

For these reasons the secondary tissues in the recent forms are to be looked upon as instances of reduction rather than cases of the inception of new developments.

T.G.H.

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THE "SEXUALITY" OF THE MUCORINEÆ.

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IT has been known for some time that zygospores of some members of the Mucorineæ, e.g., *Sporodinia grandis*, are of common occurrence and can be obtained in the laboratory with ease, while the zygospores of others are found less frequently and are obtainable by culture only with great difficulty. The occurrence of fruit-bodies in the latter forms was thus supposed to depend on some special external conditions, and various methods were proposed to ensure their production, but none of them proved certain in practice.

The key to this mystery of zygospore production was discovered by Blakeslee a short time ago and the explanation was shown to be very simple, though entirely unexpected. In 1903 Blakeslee was working on the problem of zygospore formation in *Mucor Mucedo* and obtained pure, zygospore-producing, cultures on agar. It was found that cultures from single sporangia of this material never produced zygospores; but if a mass of the mycelium was transferred as a whole, zygospores were produced in abundance around the point of inoculation, but they decreased in number as the growth widened. Again, it was found that mixed sporangial transfers from the centre of the mass gave origin to zygospores, while similar mixed cultures from the edge of the growth were unsuccessful. The culture which made clear the nature of zygospore production was prepared in order to discover whether the zygosporic activity could be transmitted through the mycelium derived from any single spore. For this purpose dilution cultures were made from mixed sporangial transfers from the centre of a zygosporic growth, resulting in one Petri dish which contained only five spores. When the five mycelia developed from these spores met, it was found that an abundant growth of zygospores occurred at the line of apposition of certain of the mycelia, while between others there was no such formation. Further, this culture showed that a certain mycelium might produce zygospores when meeting with a second mycelium, though it might be sterile towards a third mycelium, which itself was fertile with the second. The culture thus indicated that not only were two mycelia arising from different spores necessary for the production of zygospores, but also that these structures are only developed by the interaction of mycelia which are different in nature.

Blakeslee confirmed this result by numerous observations of *Mucor Mucedo*, and has extended his observations to the Mucorineæ generally<sup>1</sup>. He finds that the majority of the members of the group examined belong to the type of *Mucedo Mucedo*, and these he classes as *heterothallic* forms, since two different thalli are required for zygospore production. In these forms any given thallus bears spores which give origin to thalli of the same nature as the parent thallus.

In a minority of forms (*Sporodinia grandis*, *Spinellus fusiger*, some species of *Mucor*, *Zygorhynchus Moelleri*, *Dicranophora* sp.) the zygospores were found to arise by the interaction of hyphæ of the same mycelium, and such forms are termed *homothallic* since they possess only one kind of mycelium.

Blakeslee finds that the two different strains of the heterothallic forms can generally be distinguished by a slight difference in the luxuriance of their growth, although they are morphologically indistinguishable; but even this difference is not always present. Owing to this usual distinction the terms (+) and (—) were suggested for the two strains. The further very interesting observations were made that imperfect hybridization—the production of the early stages of zygospores which, however, never developed any further—would take place, between strains of different heterothallic forms, and between *both* (+) and (—) strains of heterothallic forms on the one hand, and homothallic forms on the other. A homothallic form sown between the two strains of a heterothallic form would thus give rise to two lines of imperfect zygospores. Owing to this power of hybridization between the various forms of the Mucorineæ, it is possible to place in their proper category of (+) or (—) the strains of such a heterothallic form as *Mucor Mucedo*, which shows no visible difference in the luxuriance of growth of the two strains. By the same means also the (+) or (—) nature of the thalli can be tested in those heterothallic forms of which only one kind of strain has hitherto been observed.

These results are of extraordinary interest and throw a flood of light on the conditions of zygospore production in the group; but the process of development of the zygospores of the heterothallic forms can hardly be on the same plane with ordinary sexual processes, as Blakeslee appears to assume. The discussion of questions of sexual reproduction is unfortunately rendered difficult

<sup>1</sup> A. F. Blakeslee. Sexual Reproduction in the Mucorineæ. Proc. Amer. Acad. Arts and Sciences XI., 1904, p. 205.



by the double use of the word "sexual." In its wide sense the term is applied to any reproductive process in which there is a union of cells, *i.e.*, a union of gametes. In its narrow sense, in which it is more satisfactorily used, it is applied only to those cases of reproduction in which there is a differentiation of the fusing gametes, the gametes being thus of two sexes. As a result of the use of the term in its wide sense we have so-called sexual processes in which there is not the slightest differentiation of sex.

Owing to the great need of a word to include all reproductive processes which exhibit gametic union, without reference to the differentiation or otherwise of the gametes, Hartog<sup>1</sup> suggested the term *syngamy*, with its adjective *syngamic*. Unfortunately this word had been used in another sense by Poulton<sup>2</sup> and published a few weeks earlier than that of Hartog. The use of *syngamy* in Hartog's sense must thus be given up, but it may, I think, satisfactorily be replaced by the term *syngamety*, with its adjective *syngametic*, as suggested to me by Professor Poulton. A true sexual process is, in this terminology, only a special case of syngamety.

That the formation of zygospores in both heterothallic and homothallic forms is a syngametic process no one would deny, but that the process is sexual (in the narrow sense) admits of very considerable doubt. Blakeslee speaks of the heterothallic forms as being uni-sexual and the homothallic as bi-sexual. Although there may be something to be said for the uni-sexual nature of the heterothallic forms, it cannot be admitted that the homothallic are bi-sexual. There is no evidence that they are otherwise than in the undifferentiated condition as regards sex, which appears to be the primitive condition of all organisms. We do not apply the term bi-sexual to the monocious species of *Vaucheria*, even though such forms bear sharply differentiated male and female cells. The fact that a homothallic mycelium will hybridize with both strains of a heterothallic form is no evidence that it is of bi-sexual nature; it would appear to indicate that it is different from them both, owing, no doubt, to its undifferentiated nature. It is really doubtful whether the term bi-sexual has any definite significance as applied to an organism. The term uni-sexual is also unsatisfactory, as applied to the mycelia of heterothallic forms.

When we study the evolution of sex, which is so well

<sup>1</sup> Quart. Jour. Micros. Science, March, 1904; published April.

<sup>2</sup> Presidential Address, Entomological Soc., Jan. 1904; published March.

seen in various groups of algæ, we find first syngametic unions in which sex has not appeared, *i.e.*, in the process of syngamesis the fusing cells are exactly alike, are in fact isogametes. In the next stage of evolution we find individuals producing two kinds of gametes, showing, in varying degrees, a larger size, a loss of activity (female), and a smaller size, and greater activity (male). The next step appears to be the production of individuals which form only one kind of gametes, either male or female. The term sex as applied to organisms thus means that there is a binary differentiation of individuals which are distinguished primarily by the fact that they bear *morphologically and physiologically different types of gametes*.

In the Mucorineæ, however, we have in the heterothallic forms a new type of binary differentiation, in which individuals (mycelia) are characterized, not by the formation of morphologically different gametes (for the fusing cells, at least in the majority of cases, are indistinguishable), but by a purely physiological differentiation, such that the gametes which lead to the production of zygosporangia are only formed when different mycelia come in contact.<sup>1</sup> In this group there is thus a *purely physiological* binary differentiation of *individuals* in relation to syngamety, a condition hitherto unknown in biology. For this reason, until further light has been thrown on the matter it would seem better to use merely the very apt terms, homothallic, heterothallic, (+) and (—) strains, and to avoid the use of the term "sexual" in relation to the mycelia in this group.

It is also interesting to note that while ordinary sexual differentiation can be related teleologically to an advantageous division of labour between the gametes, later transferred to the individuals bearing the gametes; yet the differentiation exhibited in the Mucorineæ appears to have no advantage, or, at least, no advantage which could not be gained by simple exogamy.

In a later paper<sup>2</sup> Blakeslee has made further interesting observations which, however, do not help to bring the heterothallic Mucorineæ into line with the ordinary sexual forms. He has shown that in the germination of the zygosporangium of *Mucor Mucedo* all the spores in the germ sporangium are alike, either (+) or (—);

<sup>1</sup> It must be remembered that the gametes of the Mucorineæ are coenogametes, representing, no doubt, gametangia; it is therefore possible, though not probable, that a difference in the behaviour of the two coenogametes or a difference in the structure of the constituent gametes may be observed when the zygosporangia can be more closely studied cytologically.

<sup>2</sup> Zygosporangium Germinations in the Mucorineæ. *Annales Mycologiques* IV., 1906, p. 1.

while in the germ sporangium of the heterothallic *Phycomyces nitens* there is a partial segregation of characters, both (+) and (—) spores being formed. In addition to these two kinds of spores, there are also to be found in the *Phycomyces* a few spores which give rise to *homothallic* mycelia, characterized by the occasional formation of zygospores and a peculiar habit of growth. The character of these homothallic mycelia seems unstable, for on spore-formation, both (+) and (—) and homothallic spores are produced.

One may, perhaps, suggest as a hypothesis which may possibly bridge over the gap between this group and the other sexual organisms, that the Mucorineæ are derived from algal ancestors which exhibited a differentiation of sex, both in the gametes and the individuals. The groups as a whole would then appear to be in a transition state. Some of them, the homothallic forms, have lost both differentiation of the individuals and of gametes, while others, the heterothallic, have lost the differentiation of gametes while still retaining their physiological differentiation of individuals. The view that the group is in a transition state of reduction would fit in with the fact that the genus *Mucor* contains both homothallic and heterothallic forms, and also with the fact that a heterothallic form like *Phycomyces nitens* occasionally produces homothallic strains.

V. H. BLACKMAN.

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## TWO RECENT ECOLOGICAL PAPERS.

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TWO papers have recently appeared, each of which makes an attempt to deal somewhat thoroughly with the vegetation of a comparatively limited area, and it is interesting to compare their methods and results.

One of these is "A Study of the Vegetation of the Mesa Region east of Pike's Peak,"<sup>1</sup> in Colorado, and is by Mr. H. L. Shantz, a pupil of Professor Clements, while the other is a paper on the "Ecology of Woodland Plants in the Neighbourhood of Huddersfield,"<sup>2</sup> by Dr. T. W. Woodhead, a well-known member of the young British school of Ecologists.

The "Mesa" studied is part of the "Great Plains" which have a gradual slope eastward from the Rocky Mountains, and have suffered successive erosion by eastward flowing streams, refilling of the original valleys, and fresh erosion by the streams. The soil is generally gravel mixed with a certain amount of clay and humus. The rainfall is from 32 to 43 cm. (say 13 to 17 inches), which

<sup>1</sup> Botanical Gazette **42**, pp. 16 and 179, July and September, 1906.

<sup>2</sup> Jour. Linn. Soc. Bot. **37**, p. 333. Oct., 1906.

gives, of course, a semi-desert climate. Most of the rain, however, falls from April to September, and this gives rather a luxuriant summer growth. The relative humidity ranges very low—even as low as 1% during the day in some cases,—the averages being round 50%, and saturation, giving a deposit of dew, is quite rare. There are no very extreme temperatures, but the daily range in winter is very considerable, while the difference between the daily temperature-curves of soil, soil surface, and different heights above the soil, are very striking. Exposure is of very considerable importance in altering the physical conditions. The physical factor records are taken with the elaborate thoroughness characteristic of Professor Clements' school.

The formation covering the Mesa is the *Bouteloa* (grama-grass) formation in which *Bouteloa oligostachya* is the dominant species. Clements' terms *consocieties* (corresponding to what is called an association in this country), *society* and *community* are used for various divisions of the formation, but it would have been useful if the author had devoted a little space to a discussion of the relations of these units, illustrated by the special phenomena with which he is dealing. Some of the conceptions involved are still unfamiliar to European ecologists, and that most desirable end, uniform nomenclature, which Professor Clements has so much at heart, can only be attained by repeated and convincing evidence of the soundness of the units adopted.

The formation is described under prevernal, vernal, æstival and autumnal aspects, an important and indeed essential recognition of seasonal change, which is often neglected, but nothing is said about the "consocieties" of the formation in spring and autumn, though the "consocieties" are said "at all periods to give the characteristic stamp to the vegetation," while the societies and communities are only found in each "aspect." This is probably no more than a formal omission, but it makes this part of the paper rather confusing to read. A number of "list quadrats" of the various consocieties and societies are given with the soils and water-contents for the different seasons or "aspects." These are very useful as indicating the kind of limits of water-content—usually the determining factor—under which the different species can grow and become abundant. An analysis of the figures to bring out these limits more exactly would have been welcome, as also some "chart-quadrats" to illustrate further the structure of the formation. The critical determining factors of the different units of vegetation is, of course, the most important object of exact physical factor determinations,

and till we have more evidence than is at present available of the possibility of arriving at these critical factors with some degree of exactness, the quantitative investigation of the habitat must be more or less on its trial.

The second part of the paper is devoted to a consideration of the relations of neighbouring formations to the one which is the main subject of the author's investigation, and many interesting data regarding invasion and succession are given. It seems that the pine formations of the mountains are advancing eastwards.

The weak points of the paper seem to be the absence of any special study of the natural history of the dominant plants, of the details of means of dispersal and competition, as well as the failure to analyse the physical factor data so as to determine the limiting conditions of the existence of the different types. In order to push the analysis of the vegetation to its fundamental factors such study would seem to be essential, and no ecological study that we have yet seen has carried analysis to such a point. Nevertheless what has been done in this case has evidently involved an immense amount of valuable work, and we have to thank the author for a picture of a plant-formation completer in some respects than we have yet obtained. The paper is illustrated by several good half-tones, besides the numerous tables.

Dr. Woodhead's paper originated in a desire to study more closely part of the area included in the general survey by Smith and Moss of the Leeds and Halifax district of Yorkshire. He chose an area of about 66 square miles immediately to the south of Huddersfield, extending from the coal measure shales on the east, to the high moors of the Pennines on the west, and including many woods.

The primary method adopted was to map on a large scale the distribution of the principal ground plants, such as the Bracken and the Bluebell, of a small woodland area and to correlate these distributions with those of the shade trees and the soils. In this way a very clear relation between the soil and shade on the one hand and the ground flora on the other was brought out. In a given wood, while the Bracken grew in all the soils present under oak, it was excluded by the deeper shade of elm, sycamore, and beech, while the Bluebell depended upon humus for dominance, and thinned out or disappeared over bare sandstone and clay. Another fact brought out in the same woods is the existence of a "complementary association" of *Scilla*, *Pteris* and *Holcus mollis*, whose underground parts occupy different levels in the soil, while the aerial parts flourish largely at different

seasons of the year. This association is distinguished by the author as a *meso-pteridetum*. In the *xero-pteridetum* of the drier woods, however, the association is not complementary, the Bracken rhizomes competing with Ling and Bilberry, and here sometimes one and sometimes another species is dominant.

A good sketch of the general zonation of vegetation on the eastern slopes of the southern Pennines is given.—Moss-moor, *Pteris*-slopes, heather-moor, woods with *xero-pteridetum*, woods with *meso-pteridetum*, woods without *Pteris*. The zonation is determined partly by soil, partly by exposure and rainfall.

The second part of the paper is devoted to a consideration of the effect of environment on structure in the case of some of the more wide-ranging and plastic species, such as *Pteris aquilina*, *Scilla festalis*, *Deschampsia flexuosa*, *Holcus mollis*, *Vaccinium Myrtillus*, etc. Very striking results are obtained, though on lines for the most part already well-known. The general result is that the more plastic species, both among the xerophytes and among the mesophytes, invade each others' regions to a considerable extent, and in doing so become adapted often very extensively to the altered conditions.

Dr. Woodhead's paper is illustrated by a good set of drawings of sections illustrating plasticity of structure as well as by several maps, showing the distribution of some of the principal types of vegetation, soil, etc. These maps, however, lose a great deal of their value from faults of reproduction, in the first place far too great reduction of scale, and also to some extent bad printing; some of them are in parts unintelligible. It is not creditable to the Linnean Society to fail so badly in the illustration of its Journal.

In comparing the two papers under review we see that the American excels by its wealth of exact physical factor and vegetation records, arranged according to a precise system, while the English has concentrated on particular problems. Both present interesting and valuable data, but a combination of the two methods might be expected to lead to more fundamental results. We are glad to learn that Dr. Woodhead is now at work on further study in the direction of exact physical factor determinations, and continuous seasonal observations, and we look forward to his further results with much interest. Ecology, served according to the highest ideals, is an exacting mistress, but her serious votaries may well feel that they are engaged on work which will form one of the most important parts of the future development of Botany.

A. G. T.

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LECTURES ON THE PHYSIOLOGY OF MOVEMENT  
IN PLANTS.<sup>1</sup>

BY FRANCIS DARWIN.

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II.—ON SOME QUESTIONS OF NOMENCLATURE AND METHOD.

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IN Botany, as in other sciences, there is a tendency to the multiplication of terms. In many cases this is doubtless unavoidable, for as new forms and new facts are discovered they must receive names. But too often modern terminology is but replacing old names by new and this is, generally speaking, a mistake. Then again there is the tendency to give names to phenomena which are not of sufficient importance to require special designations. But these, such as *gamotropic*, *carpotropic*, &c., commonly die a natural death, and will not be further referred to.

With regard to movement we want a terminology framed on a wider basis. We cannot dispense with such words as *pros-*, *apo-*, and *dia-geotropism*, or as *geotaxy* for swimming organisms, or *geomorphic* for the structural changes occurring in response to gravity, e.g., the growth of the peg in the *Cucurbita* seedling. But we also need a term which will embrace all these phenomena. Czapek has suggested the term *geo-aesthesia* for all cases of stimulation by the force of gravity. This is good in intention, but it is a somewhat cumbersome term, and has not as a fact been widely adopted by Botanists. *Geogenic* and *Photogenic* are occasionally employed; there is much to be said for them as being of the type of Pfeffer's terms *atiogenic* and *autogenic*, and it is to be hoped that they will come into general use. They do not, however, lend themselves to the formation of nouns; *gcogeny* or *geogenesis* strike one as awkward. Recently the term *perception* has come into use and Botanists, true to the scientific tendency to make hybrid words, are using the expression

<sup>1</sup> A Course of Advanced Lectures in Botany given for the University of London at the Chelsea Physic Garden in the October term, 1906.

*geo-perception*, and this, in spite of its barbarism, will, no doubt, be generally employed.<sup>1</sup>

I have taken the case of *geo-perception* as an instance of the classification of movement according to the nature of the stimulus. Pfeffer has suggested a fundamental application of this method in the new edition of his *Physiology*. He divides all reactions into *autogenic* and *ætiogenic*. Autogenic effects are those usually called spontaneous, such as the jerking of the leaflets of *Desmodium*. *Ætiogenic* actions are those performed at the suggestion of agents such as gravity, light, contact and the like. Klebs and other writers make the same division and describe actions as due either to external or internal stimulation. With all respect to the authority of Pfeffer I cannot believe it possible to uphold the distinction in all cases. The sleep-movements of leaves are due to the alternation of day and night, but when a plant continues to show these movements in darkness its behaviour is autogenic. Indeed it is hardly necessary to refer to a concrete case in order to show the difficulty of distinguishing sharply between auto- and ætiogenic reactions. Whenever a stimulus is repeated, its effect is due partly to that stimulus, and partly to the revival of one or more engrams which have become accessory internal stimuli. No doubt Pfeffer's classification is necessary, all I would insist on is that the distinction between autogenic and ætiogenic actions is in many cases of less importance than the bond of association which unites them.

The thesis of the "Power of Movement in Plants" is that the autogenic power of circumnutation is the basis from which the varied ætiogenic curvatures have been evolved, so that here again the two classes are assimilated rather than distinguished.

We have seen that reactions may be classified according to the nature of the stimuli, but this is not the only available method. As far as we know, the mechanism of curvature is the same whether a seedling curves geogenically or photogenically: in the case of animals the movement is the same whether executed in response to a stimulus received through the eye or the ear,—and so it is with plants. Thus from this point of view photogenic and geogenic movements fall into a single class. Is it possible to sub-divide this class by other criteria? Pfeffer has shown that it is possible. He divides curvatures into the *Tropic* and *Nastic* which may be

<sup>1</sup> In an address to Section K, British Association, 1904, I suggested *gravi-perception*. This would be convenient, but the corresponding *luci-perception* is not likely to be adopted.



distinguished as essentially directive (or Tropic), and the non-directive or Nastic movement.

The nastic movements were originally two only, viz., *epinasty* and *hyponasty*<sup>1</sup>. The essential feature was that the character of the curve is morphologically determined. Thus the epinastic leaves of *Plantago media* curve away from the axis when the plant grows on a steep bank just as they do on a level field. And the eircinate (hyponastic) curve of a fern-frond is equally dependent on morphological factors. Thus when the terms were first used, nastic was practically equivalent to autogenic. At present this is not the case: Pfeffer defines a nastic curve as one made in response to a *diffuse* stimulus. Thus to take photogenic reactions, a plant illuminated all round will give a nastic effect, whereas the great class of tropic reactions depend on the *direction* in which the light strikes the plant. The opening and closing of flowers due to changes in illumination or in temperature are described respectively as photo- and thermo-nastic, and nyctitropism has been re-christened *nyctinastism*. The paraheliotropic movements of leaves, *i.e.*, the movements occurring in bright sunshine, are often described as though the leaves directed their edges to the sun. But it is only necessary to look at a *Phaseolus* in sunlight to see that this is not so. Ewart (*Annals of Botany*, XI., p. 447) shows that in the Leguminosæ the movement is due to sunlight striking the pulvinus. He illuminated the pulvinus from below by means of a mirror and found that leaves so treated took up the normal characteristic position. The stimulus is therefore not directive, and strictly the phenomenon should be called *parahelionastism*.

Among nastic curves the distinction between auto- and ætiogenic effects has been made, and with the difficulties already referred to. Thus in *Ornithogalum* the epinasty of the leaves is induced by light (photonasty), in Tulip it occurs in darkness and would, in Pfeffer's terminology, be called *autonastism*, yet it cannot be doubted that the two cases are continuous.

In one sense there is in most nastic curvatures an autogenic element. Thus in the photonastic movements of flowers the intensity of illumination determines whether the flower expands or closes. When it opens, the surface of the petal nearest the axis grows more rapidly than the other and *vice versa* when the flower closes, that is to say the relative positions of the alternating parts of the motor mechanism are morphologically (or internally) determined, instead

<sup>1</sup> See De Vries, *Sachs' Arbeiten* i., p. 249.

of being externally determined as in tropic curves. This is implied in Pfeffer's definition of nastism, according to which the stimulus is diffuse and therefore non-directive.

Cases occur in which the nastic and tropic characters are combined. Thus certain nyctinastic plants are unable to carry out their sleeping movements on the klinostat, *i.e.*, without the action of gravity.<sup>1</sup> Under normal conditions, *i.e.*, when the plant is not on the klinostat, the sleep movement appears to be purely-nastic, since it seems to depend simply on the diminished illumination. It is true that light (apart from its direction) determines *when* the leaves shall change their position, but the direction in which the leaves move is determined by gravity, which is essentially directive in character. Here the movement is photonastic according to Pfeffer's definition, and yet it is not purely nastic, since the motor mechanism depends on the *direction* of a stimulus.

Such cases must be referred to tentatively, since more research is needed before they can be relied on, but they certainly seem to be transitions to what has been referred to as changes of tone (*Stimmung*). Thus light (apart from its direction) affects the angle at which secondary roots grow, but the actual change is geotropic.

Here I must leave a difficult question and pass on to purely tropic movements. The expression "tropic" is strictly applicable only to growth curvatures and to the variation movements of pulvini. But as Pfeffer<sup>2</sup> points out, there is frequently "no sharp line of demarcation" between tropic and tactic movements. Indeed, if we take for our criterion the directive character of the stimulus, there is no reason why the majority of tactic movements should not be called tropic, since free swimming organisms move in the direction of an external stimulus, *e.g.*, towards, or from, a source of light. But if this definition of tropism is strictly adhered to, we ought no longer to use the terms *hapto-* or *thigmotropism* for curvatures due to contact, since the organ, *e.g.*, a tendril, obviously does not place itself either parallel or at any definite angle with the direction of the stimulus. The haptotropism of a tendril, however, resembles the ordinary tropisms in as much as the stimulus determines the plane of curvature. Whether or no this form of irritability can lead to orientation depends on circumstances. If the statolith theory is correct, contact-irritability may lead to the most delicate

<sup>1</sup> Fischer, Bot. Zeitung, 1890.

<sup>2</sup> Physiology (Eng. Tr.), Vol. iii., p. 154.

type of orientation: since an apo-geotropic stem is guided to the vertical by the pressure of the falling starch-grains, as a blind man gropes his way along a wall by touch. We shall have no further occasion to refer to haptotropism, and the question of its right to a place among tropic curvatures may be neglected.

Sachs' term *anisotropic* is fortunately no longer in fashion. The fact that the root of a bean grows downwards and the stem upwards is a case of anisotropism. But it is part of our general conception of irritability that different organs may react differently to the same stimulus. The words iso- and anisotropic may be finally dismissed.

The same author's terms *orthotropic* and *plagiotropic* are on the whole useful and are in general use. An orthotropic part is one which is in stabile equilibrium only when its long axis is parallel to the direction of the stimulating agent. It may be noted however, that if the words geogenic and photogenic were employed in the sense already indicated, the terms geotropic and phototropic would include the chief cases of orthotropism, but at present *geotropic* is often employed to mean a curvature of any kind induced by gravity. Moreover *orthotropic* has the merit of defining the character of the curve without reference to the special nature of the stimulus. Pfeffer suggests *parallelotropism* in place of orthotropic: I see no advantage in the change,<sup>1</sup> and it is surely rather a cumbrous word, especially when combined, as in the expression *geo-parallelotropism*. Terminology has this, at least, in common with wit, that brevity is to be desired in both.

A *plagiotropic* organ is one that tends to place itself across the line of the stimulus, and what has been said of orthotropism applies, *mutatis mutandis* in this case. It seems to me a mistake to use *dia-geotropism* (or *transverse* geotropism) for horizontally growing organs and *klinotropism* for cases of obliquity. It is convenient to designate by a single term all the secondary roots springing from a main root, although they may take up different angles with the vertical: I prefer to call them all dia-geotropic.

Sachs' assumption of a necessary connection between orthotropic sensitiveness and radial structure, and between plagiotropic sensitiveness and dorsiventral structure, seems a mistake. It drove him to believe in an invisible dorsiventrality in secondary roots which are radial and plagiotropic. The matter should be

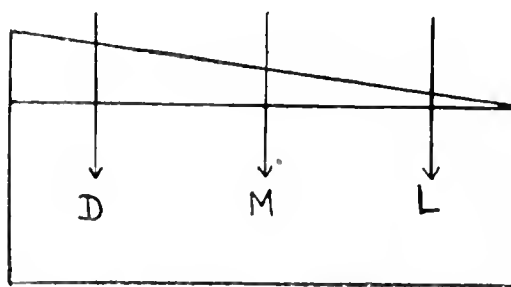
<sup>1</sup> Pfeffer however uses *orthotropism* for the straightening of an organ by one-sided growth. This use of the term seems unfortunate.

regarded from the point of view of adaptation. A leaf happens to be both plagiotropic and dorsiventral, but these qualities are distinct adaptations to illumination. A lateral root is plagiotropic in adaptation to space relations, but has no need of dorsiventrality in an environment which is the same above and below.

With regard to minor details it is no great matter whether we distinguish the different kinds of geotropism and heliotropism by the symbols  $+$  and  $-$ , or by the affixes *pros* and *apo*, although personally I prefer the latter which were suggested in the "Power of Movement." In the same way it is of no importance whether we speak of *phototropism* or *heliotropism*. The newer form is somewhat pedantic, but it has the merit of brevity and seems to be supplanting De Candolle's original term. For the same reason and for brevity's sake I prefer *dia-geotropism* to *transverse* geotropism, and I give a similar preference to *dia-heliotropism*.

With regard to the *tactic* movements of swimming organisms it has been already pointed out that they may, roughly speaking, be classed with the tropic curvatures because of their directive character. The question whether in the case of phototaxy the direction of the light is decisive was made clear by Elfving in an interesting paper.<sup>1</sup> Oltmanns<sup>2</sup> believed himself to have proved on the contrary that phototactic movements are dependent merely on the intensity of the light.

The experiments were conducted in a glass vessel rendered opaque on three<sup>3</sup> sides, the fourth side being made of a glass prism filled with a dilute mixture of gelatine and Indian ink, as shown below.



Birdseye View of Oltmanns' Trough.

<sup>1</sup> Finska Vet. Soc. Förhand. Feb., 1901, Vol. XLIII.

<sup>2</sup> Oltmanns in *Flora*, 1892.

<sup>3</sup> Oltmanns' apparatus had prisms on both of the larger sides but the form given in the Figure will serve equally well for purposes of explanation.

If we consider the light striking the box at right angles to its longer axis, it is clear that at D the light will be greatly diminished by passing through a thick layer of blackened gelatine, while at L the illumination will be much brighter, and at M there will be an intermediate condition. *Volvox* is very sensitive to differences in illumination and seeks out an optimum intensity; thus the organisms collect at M, moving from D where the light is not strong enough, and from L where it is too strong. In doing so they appear to move across the direction of incident light. But according to Elfving this is an error depending on the assumption that all the light enters the chamber at right angles to the transparent wall. Elfving points out that this is not so; an organism at M will be subject to strong oblique light from the right and weak light from the left, the resultant of these will be oblique and from the right. The organism will, in moving in the line of the resultant, travel obliquely across the long axis of the chamber and in doing so will pass through regions of varying intensity of light, in one of which it will come to a halt.

It is only necessary to imagine that light is entirely excluded at D to see that a *Volvox* at the darkened end in moving towards or from the light, would travel more or less in the line of the long axis of the chamber.

Chemotaxy is undoubtedly a case of directive action, that is to say it resembles a tropic rather than a nastic curvature. It is moreover usually comparable to orthotropic action; the antherozoids of ferns (for instance) may be seen to turn in their course and rush straight at the capillary tube from which malic acid diffuses. But this is not the only manner in which chemotaxy takes place. Rothert<sup>1</sup> has described the different behaviour of certain *Bacilli* which were large enough to be easily followed under the microscope. They do not make a directive approach to the source of attraction; if, however, they chance to come near it they do not leave it again but remain swimming backwards and forwards close to it. They are not stimulated to move in the line of increasing concentration, but a diminution of concentration affects them in a curious way: they stop suddenly and swim backwards until they again reach a region of falling concentration, when the same thing occurs. Thus they are forced to remain near the diffusing object, but, as Rothert says, the attraction is only apparent. He calls this *apobatic* chemotaxy, the ordinary type being *strophic*.

Engelmann had previously observed a similar effect with

<sup>1</sup> Flora, 1901.

*Bacterium photometricum*.<sup>1</sup> It is not attracted by light but cannot escape from a bright spot because a region of falling intensity makes it swim backwards with what has been called a *fright* or *phobic* movement (and this is perhaps a better term than apobatic). We may possibly see here a certain resemblance to nastism, since the direction of a phobic movement is morphologically determined, being a mere reversal of a previous action—a case of “backing water” in fact.

In conclusion I have to say a few words by way of introduction to my next lecture. We have seen that the principal tropic movements, namely those made in response to light and to gravity, may be looked at as parts of one phenomenon. But there is one striking difference between geogenic and photogenic action which especially concerns the methods of the investigator. I mean that he can at will remove the plant from the effects of light, but to free them from the action of gravity is not so easy. It is true that he can distribute the stimulus of gravity so that it ceases to be effective, and since I shall frequently refer to the klinostat by which this is effected it will be convenient to give a few introductory words on this instrument. The klinostat<sup>2</sup> is a clockwork arrangement by means of which a plant is kept in constant slow rotation. If the axis is vertical the effect is to diffuse, and thus destroy, the directive action of light. On the other hand if the axis is horizontal the directive action of gravity is in like manner removed. When Sachs was designing the klinostat he did not at first perceive that the horizontal instrument could be employed for both purposes—a fact which he afterwards made so familiar to us. If the axis of the klinostat is directed to the source of light the rotating plant will be subject to photogenic, but not to geogenic stimulation, while if the axis of rotation is at right angles to the line of illumination the plant will shew neither geotropism nor heliotropism.

The two theories of the action of the klinostat may be briefly stated as follows :—

(i.) That the plant is never long enough in one position to be able to perceive the stimulus.

(ii.) That the stimulus is perceived but that it affects equally all sides of the plant and is therefore ineffective.

There can be no doubt that the second is the true theory, as will be shown in detail in the next lecture. A form of the instru-

<sup>1</sup> Pflüger's Archiv, 1882.

<sup>2</sup> Sachs in his Arbeiten ii.

ment known as the *intermittent klinostat*<sup>1</sup> has been used with advantage in certain researches. We first used it to determine a small point in regard to *rectipetality*. This term (which has been replaced to some extent by *autotropism*) was designed by Vöchting to describe the fact that a tropically curved organ becomes straight on the klinostat. It was assumed that the plant is freed from external stimulus and that therefore the effect is due to an internal regulating power. But if in the case of the continuous klinostat, the stimulus of gravity is only distributed (Theory ii.) the straightening may be the result of symmetrical stimulation of an organ in an asymmetrical condition induced by geotropic curvature. This can be avoided by means of the intermittent klinostat which rotates through 180° at regular intervals. A shoot curved geotropically is fixed to the intermittent klinostat so that the plane of curvature is horizontal. "The succession of half turns prevents any geotropic distortion in the plane at right angles to the original plane of curvature, while in that plane the plant is free to increase or diminish its curvature apart from any fresh gravitation-stimulus<sup>2</sup>." Under these circumstances rectipetality occurs just as it does on the continuous klinostat. The interest of the experiment is that so far as the original plane of curvature is concerned the plant is truly *removed* from the effect of gravitation. It may therefore be said that in this respect the intermittent klinostat acts on a principle distinct from that of the continuous instrument in which the stimulus is distributed.

The intermittent klinostat may also be used to observe the effect of opposing stimuli; thus if a straight shoot is fixed to the intermittent klinostat it is subjected to prolonged alternate stimuli and falls into the curious rhythmic condition described by Miss Pertz and myself.<sup>3</sup> In the next lecture we shall see how successfully Fitting<sup>4</sup> employs both forms of instrument.

<sup>1</sup> D. F. Pertz and F. Darwin, Proc. Cambridge Phil. Soc., Vol. VII., 1891, also Annals of Botany, 1892.

<sup>2</sup> D. F. Pertz and F. Darwin, *loc. cit.*

<sup>3</sup> Annals of Botany, 1892.

<sup>4</sup> Pringsheim's Jahrb. 1905.

PTERIDOSPERMS AND ANGIOSPERMS.<sup>1</sup>

BY F. W. OLIVER.

[WITH TEXT-FIG. 32].

ONE of the great outstanding problems of Morphology now engaging the attention of Botanists is that of the origin of the dominant class—the horde of plants of complex organisation known as the Angiosperms. The revival of active interest in this question may be traced partly to the application of fresh methods to its solution, partly to the advance in knowledge of the less highly organised groups from among which the Angiosperms may have sprung. During the last few years Palæobotany has not been idle, and it is more particularly the relation of additions in this field to the Angiospermic question that will be considered in the present article.

Among these additions are two especially deserving of attention. First there is the material expansion in our knowledge of the Mesozoic Cycadophyta now focussed in Wieland's notable contribution on "American Fossil Cycads"<sup>2</sup>; secondly, there is the rapid re-arrangement of our ideas of the status of the fern-like plants of the Palæozoic, a re-arrangement from which emerges a class of generalised spermatophytes, the Pteridospermeæ.

These additions, which practically effect a change in the situation, make it necessary to consider once more what ground we have for the encouragement of the hope that some day it may be possible to link up the Angiosperms with the main series of vascular plants.

It will be convenient at the outset to glance at the chart (fig. 32) which represents in rude enough fashion the distribution in time of the great classes of vascular plants. A striking general feature (brought out by the shading employed) is the relative abundance and antiquity of the Spermatophytes in the fossiliferous rocks, a predominance which serves to emphasize the incompleteness of the records as compared with the whole scheme of plant-evolution.

Turning to the several epochs, the great feature of the Cainozoic is the rapid expansion of the Angiosperms, which, starting in Cretaceous times, soon rise to overwhelming dominance. The origin of this great group remains an unsolved mystery, for it can hardly be maintained that the supposed "Pro-Angiosperms" of

<sup>1</sup> Being the substance of a Paper read before the Botanical Club, Cambridge, December 4th, 1906.

<sup>2</sup> See Review, p. 242.



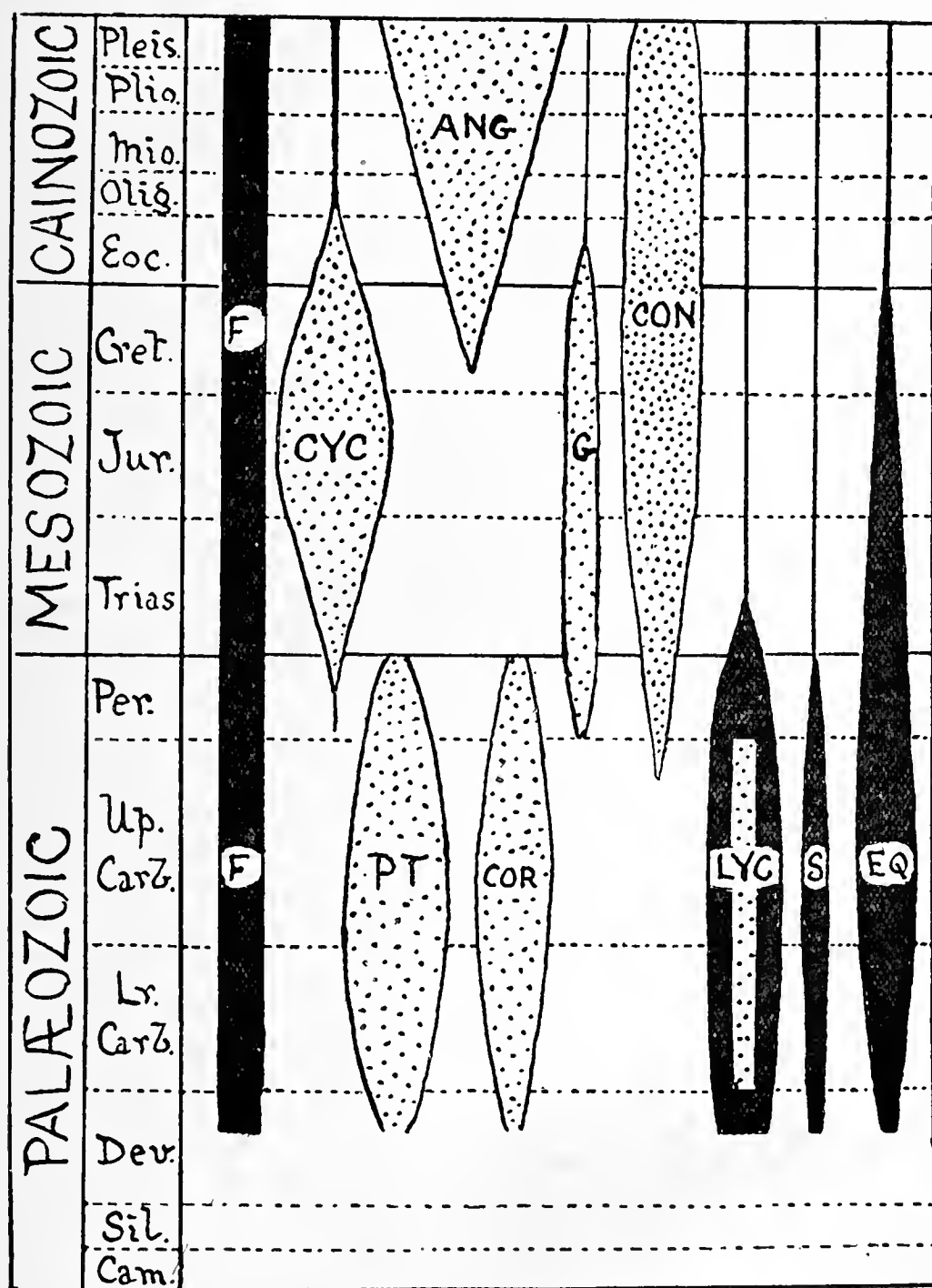


Fig. 32. CHART shewing Distribution in line of main groups of Vascular Plants. Vascular Cryptogams are drawn black ; Spermatophytes, dotted. The dotted strip on the Lycopodiaceae signifies that the seed-condition was sometimes attained. Con., Coniferales ; Cor., Cordaites ; Cyc., Cycadophyta ; Eq., Equisetines ; F., Filicinae ; G., Ginkgoales ; Lyc., Lycopodiaceae ; Pt., Pteridospermeae ; S., Sphenophyllales. (Modified from E. W. Berry).

the Lower Cretaceous have advanced our knowledge to an appreciable extent.<sup>1</sup>

The Mesozoic was the age of the Cycadophytes, with which were Conifers, some Ferns and dwindling Lycopsidea; in the Palæozoic, besides the Ferns and conspicuous Lycopsidea, there are two well-marked series of seed-plants, the Cordaitæ and the Pteridospermæ. All these spring from the lowest Palæozoic rocks where their earlier history becomes merged in obscurity.

The old generalisation that the Palæozoic was the "age of Vascular Cryptogams" remains true in part only. For whilst the cryptogamic status of the Lycopsidea has not been seriously undermined, the "Ferns" have mostly gone into solution to crystallise out in the form of seed-plants.

Notwithstanding their antiquity, it is difficult to resist the conviction that both these classes of seed-plants had sprung from fern-like ancestors. The Cordaitæ appear to have been the first to take advantage of the potentialities of the seed-bearing condition. They attained the dimensions of forest trees and massed their sporophylls on special reproductive twigs or catkins, features in which they have been followed by the more modern and, as many suppose, related Coniferæ. They do not appear to have survived the Palæozoic epoch and may be dismissed as a highly evolved group not directly concerned with the ancestry of the Angiosperms.

#### THE PTERIDOSPERMÆ.

The history of the Pteridosperms is very different. Though having in common with the Cordaitæ the same type of seed, they retained the habit and much of the anatomy of Ferns. They are essentially seed-plants improvised out of Filicinean ancestors and have been aptly described as "Fougères à graines." One might almost speak here of Spermatophytic Ferns as opposed to Cryptogamic Ferns.

The discovery of the group was strangely belated owing to the facility with which the seeds were shed. Long ago some of those accustomed to handling Coal-Measure fossils seem to have suspected that there was something anomalous about the "Ferns," as we may gather from the following passage describing an exhibit at the meeting of the British Association at Birmingham (1849):—"R. Austin, Esq., exhibited a specimen of a Fern from the English

<sup>1</sup> Cf. A. C. Seward, *NEW PHYTOLOGIST*, Vol. II., p. 243.

Coal-Measures bearing abundance of fructification. He did this as the rarity of the occurrence had led him to suggest, at a previous sitting of the section, that in these latitudes the ferns of the coal-beds did not fructify on account of the low temperature in which they existed<sup>1</sup>." Stur went much further and definitely excluded a large number of genera of foliage from amongst the ferns proper (1883). Then came the anatomical investigation of the vegetative organs of these forms, and the establishment of a provisional group, the Cycadofilices, depending on the anatomical characters. Finally, seeds were discovered with tell-tale fragments of cycadofilicinean fronds attached, thus proving the existence of a remarkable class of seed-plants now known as the Pteridospermeæ.

Could a Botanist have seen these plants growing side by side with cryptogamic ferns, no essential difference in habit would have been apparent; merely the existence of a reproductive peculiarity. The difference between them was analogous to that which we now find between ordinary seed-plants and certain of the Mangroves which are viviparous. The difference here is a trivial reproductive modification to be correlated with a special type of habitat, as is currently supposed. But it is just conceivable that this modification might become important in certain eventualities. However, the point to be noted is that seed-bearing at its inception was effected without marked change in the habit of the plants participating.

By the use of the words "at its inception" it will not be understood that Pteridosperms have stood still. The Lagenostomas, Trigonocarpons, and other seeds that belong to the Pteridosperms are fairly advanced structures of the same order of specialisation as those of living Cycads, for instance. Exactly how these seeds were fashioned out of the ancestral sporangia there is no available direct evidence to tell us. The examination of petrified specimens shews them to be complicated structures—with their pollen-chambers, integuments and vascular systems—hardly paralleled in living plants outside the Cycad group. This early complexity may well have been an essential factor in the success of this rather momentous new departure, for it seems to have secured the conditions for fertilization in which the necessary water was under control. To state the matter in a slightly different form, plants that had acquired the seed-habit must have been able to spread to places other than such as provided the necessary conditions for the ordinary cryptogamic type of fertilization, an advantage emphasized at the present

<sup>1</sup> Henfrey's Botanical Gazette, Vol. I. (1849), p. 305.

day by the relatively conspicuous part which annuals play in desert floras.<sup>1</sup>

Additional characters, such as the resting embryo, may have been acquired later, for embryos have not been found in Palæozoic seeds. In time also, with the assumption of some of its functions by other structures, the seed evidently underwent considerable simplification.

Another consequence that followed in the wake of the seed-habit was the impetus given to advancement, as is well illustrated by the Mesozoic Cycadophyta to be referred to below.

If reference be made to the chart (fig. 32), it will be noticed that the Filicineæ are represented as a continuous strip of even width. At present, whilst our notions respecting this series are recovering but slowly from the rude shock dealt by the far-reaching nature of the pteridospermic encroachment, it seems hardly possible to attempt anything more definite. From a recent authoritative statement of the position it seems evident that, although true Cryptogamic Ferns existed in Palæozoic times, some time must elapse before it will be possible to speak with confidence of their nature and extent.<sup>2</sup>

#### VASCULAR CRYPTOGRAMS AND THE SEED-HABIT.

Before leaving the more primitive representatives of the Pteropsida-phyllum some reference may be made to a feature in which they contrast in marked degree with the Lycopsida, *viz.*, the lack of concentration and differentiation of their sporophylls. On the whole, the evidence goes to shew that in these megaphyllous forms we have to deal with relatively generalised and primitive types in which the form and aggregation of the sporophylls shew little specialisation in connection with the sporangium- or seed-bearing function.

In the case of the Lycopsida the sporophylls are characteristically massed into cones, and shew an evident relation both in form and extent to spore production.

In addition therefore to the more obvious differences in structure which form the basis on which Pteropsida and Lycopsida are discriminated, there seems to be some grounds for regarding the two

<sup>1</sup> Thus Schweinfurth, in W. P. May's "Helwân and the Egyptian Desert," enumerates 191 species as constituting the desert flora of Helwân, of which 116, *i.e.*, 60% are given as annuals.

<sup>2</sup> D. H. Scott, in Lott's *Progressus Rei Botanicae*, Vol. I., pp. 177-189.

series as being in somewhat different phases of evolution or as having responded to the stimulus of spore- (or even seed-) production in a rather different way.

The Lycopsidea in the cryptogamic condition seem to have undergone marked adjustment and specialisation in connection with the spore-bearing function, for a parallel to which, in the Pteropsid-series, one has to turn to fairly advanced spermatophytes such as the Cordaites and Cycadophyta.

The Lycopods and Calamites reached their zenith in Palæozoic times, when they attained the dimensions of forest trees. For some reason or another they seem to have exhausted their resources of adaptation upon the cryptogamic method, so that they were without the needful reserve of plasticity to follow up the beginnings of seed-production upon which some of their representatives are known to have stumbled (*Lepidocarpon*).

The megaphyllous forms, on the other hand, behaved in a different way. To them the cryptogamic state was not a phase upon which to expend themselves. They retained their full plasticity till the supreme moment of becoming seed-plants, and only then, and without hastening, did they begin to modify and specialise their organs of fructification.

As an illustration of the remarkable adjustment in matters of sporangial details of which palæozoic Lycopods were capable, the cones known as *Spencerites* and *Lepidostrobus*, respectively, may be taken. The former is remarkable for the distal attachment of the sporangium to the sporophyll, where it is inserted upon a cushion which has been compared with a Sphenophyllaceous sporangiophore.<sup>1</sup> In *Lepidostrobus*, on the other hand, the radially elongated sporangium is attached throughout its length to the upper surface of the pedicel of the sporophyll. This difference—not improbably of nutritive significance—offers some analogy with the relations of nucellus and integument in the two groups of Pteridosperms: Neuropterideæ and Lyginodendreæ. In the former the nucellus stands free within the integument (*Trigonocarpon*, *Stephanospermum*), whilst in the Lyginodendreæ (*Lagenostoma*) a large measure of coalescence obtains, so that only the tip of the nucellus is free, a condition also found in living Cycads. The free condition is presumably the more primitive, and in this connection it would be of some interest should *Spencerites* turn out to be the cone of

<sup>1</sup> D. H. Scott, loc. cit., p. 170.

*Bothrodendron*<sup>1</sup>; for this genus, known in Devonian rocks is among the most ancient of which the remains are preserved. This digression will serve as an illustration of the way in which the sporophylls of the Lycopod line have become involved and modified in connection with the cryptogamic phase in a manner finding its parallel in other evolutionary lines in the parts associated with the seeds themselves.

#### THE CYCADOPHYTA.

We turn now to the great series of the Cycadophyta, which formed such a predominant portion of the Mesozoic vegetation and of which our existing Cycads represent the surviving residuum.

Between this series and the Pteridosperms the closest relationship is generally admitted to exist, a relationship which is reflected in the habit, vegetative anatomy and seed structure. In view of the many points of agreement, it is reasonable to suppose that the Cycadophyta may have sprung from the Pteridosperms, though at present it is hardly possible to indicate the exact line or lines of descent.

Within the limits of the Cycadophyta two well-marked families have been recognised: the Cycadeæ and the Bennettitæ. The former of these is best represented by the surviving Cycads, the latter by Bennettites and the rich series of Cycadeoideas from the Jurassic rocks of N. America. It is probable, notwithstanding the unusually full information now available on the representatives of these two families, that our acquaintance with the range of variation presented by the Cycadophytes as a whole is very incomplete.

*Cycas* itself affords what may be an interesting survival from the Pteridospermic stage in its unspecialised fern-like carpels, which, though produced in periodic rotation with the vegetative leaves, are borne on the main axis of the plant. Among other representatives of the group a more advanced condition is met with, both in the specialisation of the sporophylls and in their concentration upon special axes to form definite cones. On the whole the Cycads afford an example of an easily recognisable derivative of the Pteridosperm-plan in which a certain amount of concentration and specialisation has taken place. In this respect the group is somewhat on the level of organisation of a palæozoic Lycopod, though, in the latter case, we are of course dealing with plants of cryptogamic status.

<sup>1</sup> D. H. Scott, loc. cit., p. 171.

In the Bennettitales on the other hand the great morphological feature, as compared with Cycads, is the high degree of modification met with in the reproductive organs. Whilst the vegetative habit is comparable to that of a dwarf and robust Cycad, and the anatomy is organised on essentially Cycadean lines, the fructifications take the form of laterally placed "buds" or "cones" usually found slightly projecting from between the persistent leaf-bases. The fructification consists of a short axis terminating in a convex receptacle. The proximal parts bear numerous scale-leaves, which are clothed with ramenta, recalling similar structures in recent ferns and in such Botryopterids as *Zygopteris corrugata*. Between the enclosing "bracts" and the convex receptacle, the American specimens shew a whorl of from 10—18 frond-like microsporophylls. These remarkable organs, whose discovery and description we owe to Dr. W. R. Wieland, are pinnate in form and coalescent below; the pinnae bearing double rows of synangia which contain the microspores. With the shedding of the spores the frond-like portions of the sporophylls withered or fell away leaving their coalescent bases as a circular collar or disc around the contracted neck of the convex receptacle. The receptacle itself is closely packed with the well known seed-pedicels, each of which ends in a straight seed, and interseminal scales which become enlarged distally to form a sort of pericarp, which, whilst enclosing the seeds, allows their micropyles to reach the surface. Thus in a few words are outlined the salient features of the "bisporangiate strobilus," with the reconstruction of which Dr. Wieland has crowned the first stage of his labours on the American Cycadeoideæ.

We now come to the question of the morphological interpretation of this fructification. Whether it is to be regarded as "an axis beset with sporophylls," *i.e.* a flower, or whether, on the other hand, it is really a much more complex structure, *i.e.* an inflorescence or branch-system shewing extreme reduction. Even when the female fructifications of *Bennettites* alone were known, the possibility of a close approximation to an angiospermous flower was recognised.<sup>1</sup> Now that we have precise details of the microsporophylls, the view taken by Dr. Wieland, that we have here a hermaphrodite flower, will meet with very general agreement. Looked at broadly and having regard to the pteridospermous affinities of the Bennettitæ this interpretation seems irresistible. To take the other view and read a "cyathium" into its structure seems to

<sup>1</sup> See Scott's "Studies in Fossil Botany," pp. 474—478.

verge on the gratuitous. Regarded as a flower, we see in it a remarkable combination of primitive and advanced characters. The microsporophylls of *Cycadeoidea* if combined in one plant with the seed-seales of *Cycas* would give us all the essentials of a quite generalised Pteridosperm. But the Filieinean affinities are so evident as hardly to need further emphasis.

The great interest to many, and among them the present writer, will be the significance of this hermaphrodite flower from an Angiospermous point of view. Does its existence tend to bring Angiosperms into the Fern-Pteridosperm-Cycad line? The flower is admittedly a gymnosperm in that pollination is direct, but one's faith in the old shibboleths has in these days received many shocks. As a feature of taxonomic importance the existence of secondary thickening has lost all its former significance. The possession of seeds, again, is readily admitted to be no mark of affinity. Is it possible that Angiospermy and Gymnospermy as differential criteria of affinity will have to go too?

Whatever else one may think of this flower it cannot be regarded as that of a quite typical Angiosperm, although Wieland has compared it appropriately enough with the flower of a Magnoliaceous plant.

Its great interest and value seems to be that whilst just missing the Angiosperm it shows how close the Cycad line could come to realising it. It is indeed the key to the Angiosperms; when that is recognised the rest is easy.

One would be tempted to speak of the two series of Cycadophytes by the names Gymnocycad and Angiocycad respectively, were it not for a reasonable confidence that there must be still other forms lying hidden in the earth's crust even better qualified than *Cycadeoidea* to bear the designation Angiocycad. It is possible, no doubt, though it seems almost incredible, that a flower with perianth, stamens and gynæceum in proper relative position as in *Cycadeoidea* should have been produced except in a line very closely related to that which led to the Angiosperms.

That the actual difference between Angiosperms and Gymnosperms in the early days was very slight will be realised when some of the minor points of structure in *Cycadoidea* come to be worked out in detail. In this connection attention may be drawn to a structure which Dr. Wieland conjectures may be the trace of an extra-seminal wrapping having its insertion at the distal end of the



seed-pedicle just below the chalaza.<sup>1</sup> This, in guarded terms, is compared with the cupule of *Lyginodendron* (Lagenostoma).

No doubt the cupule of *Lyginodendron* holds out the possibility of being the kind of structure that might have been the precursor of an enclosing Angiospermic carpel in some lines of descent, as Mr. Arber has pointed out;<sup>2</sup> whilst in other cases, especially where there is crowding as in *Cycadoidea*, or (to go further afield) in the analogous case of the aril of *Phyllocladus*, this supposed primordial carpel might have dwindled to the insignificance of a vestige.

It is quite conceivable that in some undiscovered, but allied, branch of Cycadophyta this organ might have increased in importance by the assumption of stigmatic functions; if so, this hypothetical group would make a strong bid to be the real Pro-Angiosperms.

At present, however, it is premature to draw any conclusions whatever from an organ so obscure as the cupule-like envelope of *Cycadoidea*, for the whole question being of the most fundamental and far-reaching significance, conclusive evidence alone can serve our purpose. When the developmental stages of *Cycadoidea* come to be worked out, perhaps fresh light may be thrown on the question of the existence of a "cupule" in the group.

Hence it would appear that whilst the latest work on the flower of *Cycadoidea* brings the Filicinian seed-line appreciably nearer to a junction with the Angiosperms, there still remains a hiatus to be bridged. Further back, the Pteridosperms shew us the lines along which the Cycadophyta may have arisen from the archaic Ferns (the Primofilices of Arber), of which the Botryopteridæ is the only group at all well recognised. But here again we still await the linking forms, representatives shading down into the Ferns below and into the Cycadophytes above.

Apart from the capriciousness of fossilisation, one is inclined to suspect that such types may have been rare in the actual floras. And further, when—by whatever means—such a one had given origin to the beginnings of a new class, extinction would await the parent form when subject to competition with its offspring. This perhaps is the explanation of the survival to our days of the non-Angiospermous branch of the Cycadophyta: unlike the Bennettitales they evaded direct competition with the Angiosperms.

<sup>1</sup> G. R. Wieland, loc. cit., pp. 120 and 234.

<sup>2</sup> E. A. N. Arber. "On Some New Species of Lagenostoma." Roy. Soc. Proc., Series B., Vol. 76, p. 256.

It is true that in Fossil Botany some leeway has been made up in recent years, and unknown families and even classes have been reconstituted. But if the rate of progress has been temporarily accelerated, we cannot on that account expect—what seems so rare in analogous cases—that all our missing links should come conveniently to hand. We shall have to rest content to draw such conclusions as we may from an increasing knowledge of the range of structure of the great groups as they succeed one another in time. Judged by this modest standard, our knowledge of the main phases in the phylogeny of the higher plants has advanced amazingly, and it may be possible in the not very remote future to trace with some confidence the main lines that have been followed by the Angiosperms in the hitherto obscure process of their evolution.

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#### AMERICAN FOSSIL CYCADS.

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**D**R. G. R. WIELAND'S years of industrious labour on the Mesozoic Cycads are at last culminated by the publication of a work, the interest, beauty and importance of which it is difficult to over-estimate.

After the knowledge we possess of modern living Cycads and the recent detailed information to hand as to the nature of their Palæozoic ancestry, the Pteridosperms, what could be more opportune than this timely appearance from America of a fund of instruction with regard to the character of plants pertaining to the same great group, but occupying the vast time-period which we call the Mesozoic, intervening between the Palæozoic and the modern epoch.

The Mesozoic Cycads, known in America as the Cycadeoideæ and in this country as the Bennettiteæ, possess features of extraordinary interest and uniqueness which mark them out as belonging to a distinct and independent line of evolution among the Cycadophyta. Nevertheless, they exhibit characters which clearly relate them on the one hand to modern Cycads and on the other to the ancient Pteridosperms.

In the introductory chapter Dr. Wieland affords us an excellent account of the various discoveries and collections of the Cycadeoideæ, an account which reveals the world-wide distribution of the group during the Mesozoic period,

Thanks to the labours of himself, Professors Lester Ward and O. C. Marsh and others in America, these plants are now known from the Trias of Pennsylvania and N. Carolina, through the Jurassic of Colorado and the Potomac Formation of Maryland, to the Upper Jurassic, Wealden or Lower Cretaceous of the Black Hills of S. Dakota and Wyoming. These last localities have been by far the most fruitful source of the interesting material which forms the subject-matter of the volume before us.

In the old world they have been found in the Gondwana system of India; in England the researches of Mantell, Buckland, Carruthers, Williamson, and Seward have shewn how they occur in the Lias, Wealden and Lower Greensand. Morièrè and Lignier described French specimens from the Middle Lias and Oolite; Walch, and later Ward, the specimens from Galicia; and Capellini and Solms-Laubach the two specimens known from Italy. At the conclusion of this chapter the author points out how large a part of the field is as yet wholly unexplored, citing the greater part of the Rocky Mountain Chain, the western slopes of the Andes, the mountain chains of Asia, &c., &c., in this connection.

Chapter II. is devoted to a consideration of the mode of preservation and the external characters of these plants. It is interesting to note how a study of the mode of, and conditions attending, fossilisation<sup>1</sup> in the different localities is very useful for the comprehension of the external conformation and appearance of the various trunks. These are mostly bulbous, or sub-spherical in outline and were much given to branching. Unbranched forms also occurred; of these some, e.g., the Jurassic *Cycadella* were, like the modern *Bowenia*, small and rarely branched; others, e.g., *Cycadeoidea gigantea* and *Fenneyana*, were columnar and probably reached a height of two to three metres.

The great diversification of trunk-form, far surpassing that of modern Cycads, stands out as a striking and important fact.

Chapter III. deals with the methods of section-cutting.

The second section of the book treats of the vegetative features of the Cycadeoideæ, of which Chapter IV. gives a detailed description of the trunk-structure, including the armour, the leaf-bases, the cortex, the xylem zone, and the medulla. The great development of the woody cylinder, comparable to that of *Cordaites*, is characteristic of *C. Fenneyana* and *C. ingens*.

<sup>1</sup> Silicification, resulting in the formation of almost perfect casts of the tissues, was the process concerned.

Chapter V. is concerned with the subject of the foliage of these plants ; owing to the evidence accruing from mature imprints as well as exact details of pefoliation and frond structure, "the picture of Cycadeoidean foliage becomes unexpectedly complete." It is owing to the *preceding* dense enveloping growth of ramentum, that the various foliar organs have been so well preserved. In the case of the specimen *C. colossalis* "there appears to be more or less of a hiatus in growth between the series of partially emergent fronds and the ramentum arcae immediately succeeding them." "Hence we cannot doubt that in many of these plants growing amidst the generalised tropical conditions of the Upper Jurassic as far to the north as the Black Hills (44°N), the wilting down of old leaves and the growth of new crowns mainly proceeded with the seasons."

Section III. deals with the reproductive structures, and is, perhaps, the most absorbing and interesting part of the whole work. It is no exaggeration to say that our author, as is evinced in this section, has risen, in the triple labour involved in the collection of the material, restoration of the structure, and detailed description of the latter, to a high level of merit as a botanical investigator and writer. As regards the ovulate cones with which Chapter VI. deals, he abundantly confirms and extends the able researches and descriptions of Carruthers, Solms-Laubach, and Lignier. Side by side with his lucid explanations, we are supplied with such a wealth of accompanying text-figures and photographs, as to render the comprehension of the complex structures treated of comparatively easy. One of the exhilarating features of our author's new treatment of this subject consists in the great *variety* of types now for the first time presented to our view, a variety concerned more especially with the relative length and development of the peduncle, and of the seed-bearing part of the axis. But by far the most important result accruing from the investigation of the new material is that these wonderful cones were all, completely or incompletely, *bisexual* ! This is shewn by the presence of the "hypogynous annular shoulder indicating the earlier attachment of a dehiscent staminate disk" intervening between the highest of the enclosing bracts and the lowest seed-bearing pedicel. The following statement of the author is also suggestive: "while a bisexual strobilus is primarily indicated, the form of fructification is precisely the one capable of most varied phases of monœcism and diœcism"; and "while diœcious and monœcious or mixed bisexual forms are suspected to

be present, no such have actually been determined." In the *mature* ovulate cones only these withered disks occur, indicating a pro-tandrous condition of the cone. The dicotyledonous embryos, already well-known in the seeds of the European specimens of these plants, also occur in the American species; the discovery of pre-embryonal stages exhibiting "a partial agreement with Ginkgo in which there is no intervention of suspensors in the formation of the embryo from the homogeneous mass of large-celled tissue constituting the pro-embryo or protocorm" is another of the weighty results of our author's work. "And," he adds, "there is probably at hand material which, when once fully elaborated, will disclose the main outlines of embryogeny in the Cycadeoideæ."

But the climax of interest is reached in Chapter VII., where, by dint of ingenious analysis of highly complex conditions of structure and of an equally ingenious synthesis shewn in the striking and beautiful restoration-figures, the author describes for us the *male* reproductive organs as they occur in these remarkable pro-tandrous, bract-ensheathed "flowers." These silicified flowers only occur in the bud-condition. "The ovulate cone is elongate, and its ovules are young and borne on very short pedicels." "The staminate disk is formed by a series of from ten (in *C. fenneyana*) to eighteen or twenty (in *C. dacotensis*) once-pinnate fronds with a strong basal adnation of their petioles continuing nearly to the summit of the central cone." "Each frond bears about twenty pinnules closely set with two sub-laterally attached rows of distichous and sessile synangia, and is of partially circinnate prefoliation, being once inflexed, so that the upper third of its length lies with the ventral surface of the rachis appressed to the central cone, the fertile pinnules being folded back in pairs between the ascending and descending limb of the rachis. And since the pinnules follow in close order, all this intervening space is densely packed with synangia, the sporangial loculi of which are often filled with pollen." It is pointed out that "the compact bud-like form and fairly mature stage of growth in a protected position were very important factors in preservation." The synthesis of restored structure has been chiefly attained by means of a remarkable series of transverse sections extending from the level of the peduncle upwards, text-figures of which are given.

Such nightmare inexplicabilities as the "pyriform axis," "carpellary disk," &c., of Williamson's "*Zamia gigas*," described by him in the darker period of palæobotanic research, appear, in the

light of modern scientific method and knowledge, to receive for the most part a rational form and explanation in the structure of the bi-sporangiate cone.

Chapter VIII. deals with the young ovulate axis.

Section IV. comprises the important subject of relationships, the heading of Chapter IX. being: "Existing and Fossil Cycads Compared." It contains a thorough and comprehensive account of the distribution, external morphology and anatomy of modern Cycads, following on which is a summary of the relationships of Cycadeoideæ to existing Cycads, the conclusion from which is, as regards the vegetative structure, that there is not a single vegetative character of the former which does not find a near analogy in the latter; that "probably complexity of leaf-traces in the line leading into the modern Cycads would have been the only difference that had yet arisen in the Cretaceous ancestry of the latter in advance of the more ancient vegetative features of the Cycadeoideæ"; that probably no macroscopic or microscopic feature would have been present in early Triassic times in such a type as *Anomozamites* which is wholly absent in modern Cycads; and that "the far-reaching identity and similarity in the vegetative structures of the two Cycadean groups" could not be "the homoplastic result of physiologic conditions of growth and evolution alone, and merely the result of parallel development from two distinctly and remotely separated fern-groups." "The reasonable hypothesis is that the ancestral line from which the Cycadeoideæ and existing Cycads sprang remained single and homogeneous until the major outlines of leaf and stem similarity now common to the two groups were established." The same conclusion is reached from a comparison of the reproductive parts.

The author's final conclusion is that "the Cycadeoideæ, as an ancient apposite of the Cycadeæ, find their appropriate place among the true Cycadales," inasmuch as he regards the two groups as separating off as early as the Permian from a common ancestor in the Pteridosperms, which in their turn were derived from a closed homogeneous Marattiaceous complex, in which heterospory had been evolved.

The last Chapter, X., is divided into three parts, the first treating briefly of the Fern-Cycad relationship; the second of "Sporophyte Reduction correlated with elimination of separate prothallial stages and evolution of seed-bearing quasi-ferns"; the third of the "ultra-relationship of the Cycadalean Gymnosperms (or the

Cycadeoid-Angiosperm juxtaposition).” In this last paragraph he points out the absence of parallelism in the evolutionary development of the mega- and microsporophylls respectively of the Cycadeoideæ; for here the microsporophylls have remained primitive, while the female apparatus has become greatly reduced and modified; conversely in the modern *Cycas* it is the megasporophyll which has remained primitive, while the microsporophylls have become greatly reduced and changed. Yet the Cycadeoid microsporophylls, although of such primitive type in themselves, have adopted the *cyclic* arrangement, which, as the author points out, “have made possible a wholly new series of reductions.” He proceeds to imagine how from certain Cycadeoid cones with spirally-arranged microsporophylls a reduction of these latter to a filamentous staminate form might have occurred, giving rise to a type of flower like that of *Liriodendron*. Again “striking analogies to living angiosperms are suggested, no difference whether we fasten our attention upon one set of characters, and *Liriodendron* be called to mind, or upon another, with the result that the male and female catkins of Amentaceæ first suggest themselves, or upon a third set that call to mind some other list of characters that must have been present in the countless members of a great proangiosperm complex.” “What right would we have to look for instance upon the bifurcate stamens of *Ginkgo* as separated by an unbridgeable hiatus from those of the multibranched stamens of *Ricinus*? Assuredly none. For the purposes of broader generalisation, fern-like fronds upon which doubtless were borne the pollen of *Lyginodendron*, the staminate fronds of *Cycadeoidea* of true Marattiaceous type, the mega- and microsporophylls of *Cycas*, the stamens of *Cordaites* and *Ginkgo*, and finally of *Ricinus* and *Lyginodendron*, all belong to a series. Nor is there from a plain point of view an unbridgable gap between the staminate disk of *Cycadeoidea* or that of *Welwitschia*, for the latter could arise similarly to one of the hypothetical one-seeded and bi-sporangiate forms of the Cycadeoidean alliance by one of the simplest of all evolutionary processes, *viz.* increased number of flowers to the plant and decrease in bulk, until there was left of each original frond but a single filament bearing a pair of pollen-sacs (as in *Ginkgo biloba*), and finally but a single pollen-sac, the filament retaining the original cyclic arrangement of the fronds from which they were derived.” Finally, he submits that in the Cycadeoidean flower, “the juxtaposition of parts is exceedingly suggestive of the pos-

sibility, if not the manner as well, of angiosperm development directly from filicinean forms."

With the views above expressed the reviewer heartily agrees and recognises in the "flower" of *Cycadeoidea* a development *parallel* and *analogous* to that of an Angiosperm. From the data to hand as to the derivation by way of extreme *reduction* of the sporophylls of modern Cycads from those of Pteridosperms, we must regard the simple one-seeded megasporophyll of *Cycadcoidea* as a striking instance of excessive reduction while retaining the radial symmetry of structure which it appears to inherit from the sporangium-bearing pinnule in the far-back Fern-ancestor; but this condition is far removed from the highly advanced and modified structure of the Angiospermous carpel. Still less does the microsporophyll of *Cycadeoidea* bear any resemblance to that of an Angiosperm, which latter, in course of its probable great reduction and simplification, has, like the megasporophyll of *Cycadcoideæ* retained primitive radial structure. Nevertheless, that the highly reduced and congested cone of *Cycadeoidea* is well on its evolutionary way towards the "flower"-structure of an Angiosperm, as shewn by the mode of juxtaposition of the mega- and mierosporophylls and by the cyclic arrangement of the latter, the reviewer verily believes; yet really not more so than, if as much as, the cones of modern Cycads, for he still regards the cone of *Cycadeoidea*, as, on the whole and essentially, more *primitive*, than that of modern Cycads, with the exception of the female side of *Cycas*.

This epoch-making work, for it is nothing less, should be studied by all interested in the evolution of plants, for embedded in its pages, and, indeed, involved in the very nature of the subject matter treated of, are problems of wide and general importance for the student of evolutionary development. For example much room for thought is afforded by the question, how far and to what extent is "reduction or simplification of structure an accompaniment of evolution?"

The book contains 246 pages of text, 138 text-illustrations, 50 plates of excellent photographs, with a very full description of each; a Bibliography, in which 219 works are cited, and an adequate index.

Dec. 4th, 1906.

W.C.W.

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THE FLORA OF LAKE TANGANYIKA.

AT the Linnean Society on December 20th Dr. Rendle and Mr. G. S. West gave some account of the botanical results of the Third Tanganyika Expedition, conducted by Mr. Cunningham in 1905-6.

It will be remembered that as a result of his two expeditions to the great Central African lake, Mr. J. E. S. Moore came to the conclusion that its peculiar fauna showed distinct traces of marine origin, and put forward the hypothesis that the lake had been isolated from the sea in Jurassic times and had ever since retained a portion of the marine fauna which it possessed in that epoch. Imaginative botanists thereupon dreamed dreams of freshwater Brown and Red Seaweeds inhabiting the lake and presenting all sorts of unexpected possibilities in algal evolution.

Mr. Cunningham's extensive collections of the flora of the lake do not however support this theory. The account which Dr. Rendle gave of the aquatic flowering plants showed that for the most part they are widely distributed tropical types, and in many cases are found also in Nyassa and Victoria Nyanza. Furthermore of those which were found in Tanganyika alone, nearly all are known from other parts of the world and certainly do not suggest a marine origin. Of these *Naias marina*, for instance, in spite of its name, is found not only in the Norfolk Broads and the Norwegian fiords but also in the Swiss lakes. The cosmopolitan *Potamogeton pectinatus* and the very common tropical *Jussiaea repens* are other examples.

When we turn to the Algæ the case is not much stronger. Mr. Cunningham made a very large collection of the plankton both from Nyassa and Tanganyika, and in addition to a number of cosmopolitan forms such as *Pediastrum*, *Botryococcus*, *Melosira*, *Stephanodiscus*, *Anabæna flos-aquæ*, some more restricted type, such as the diatom *Surirella Nyassensis*, and *Chodatella subsalsa* a minute green plankton-form with long bristles, hitherto known from the shores of the Baltic, were found. Also a new tubular alga, constricted at intervals, which is to be called *Sphinctosiphon*. Out of the whole number of plankton algæ found in Tanganyika a very large percentage are certainly peculiar to it, but it cannot be said that the case for the marine origin of its algal flora has been in any way made out.

Mr. Cunningham said that Tanganyika, shut off from communication with other waters, with a high rate of evaporation and a small drainage area, had evidently for a long time been decreasing in volume and probably increasing in salinity. The older travelers always said its water tasted peculiar. Then apparently a time came when it was suddenly filled up by waters from the north, and the lake also acquired an outlet to the Congo basin. Now again its level is evidently lowering again, for it is easy to see traces of the lake many feet above its present level.

Thus it may well be that the fauna and flora have had to adapt themselves to increasing salinity, and the long period of isolation which the lake has evidently undergone has, no doubt, had a differentiating effect on the inhabitants. This would account for the large number of endemic species of animals and plants. Of a specifically marine origin Mr. Cunningham's botanical results, at least, seem to furnish no evidence.

## THE NUCLEUS OF THE YEAST PLANT.

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On the Structure and Biology of the Yeast Plant (*Saccharomyces Cerevisiae*). By Fred Mutchler. *Journal of Medical Research*, Vol. XVI., Nov., 1905. Boston.

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ON account of the diversity of opinion which exists regarding the nucleus of the yeast plant, attention may be drawn to the results embodied in the above contribution, which appears in a journal not generally read by botanists.

The first part of the paper enters into the consideration of the structure of the yeast cell. The cytoplasm is more or less reticulated, vacuolated or areolated, the meshes are very close and the areolation is much more regular than in the animal and vegetable cells studied at the same time and prepared in a precisely similar manner.

The nucleus occupies the centre of the cell and is relatively larger than any other part. The measurements given are surprising; the average diameter of the cell itself is given at seven microns, and of the nucleus, five microns. The nucleus is closely areolated with a fine net-work which exhibits a great affinity for gentian violet.

Surrounding the nucleus is a distinct nuclear membrane, and in close association with it are a varying number, from six to ten, of small, but definite, granules. Sometimes these may be scattered throughout the cell but usually are situated "immediately under the membrane."

No evidence of karyokinesis has been observed, and it is believed that the division of the nucleus in all cases is direct.

The second portion of the article deals with the effect upon the cell of various substances which included a large number of metals, formalin, hydrogen peroxide, acetic, picric, and other acids, alcohol, and, finally, many anaesthetics.

The conclusions drawn from these experiments are as follows:—

(i.) The form of *Saccharomyces Cerevisiae*, having remained constant under the conditions imposed, leads to the conclusion that it is not a variable species.

(ii.) Any variation in form is due to the inherent nature of the cell rather than to external conditions.

(iii.) Variation in the size and in the rate of growth of the cells is readily produced by changes in the conditions under which they grow.

(iv.) Anaesthetics do not permanently destroy the growth or reproduction of this species.

